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The Effect of Reduction of Fishing Effort on Yield[1]

By Syoiti Tanaka[2]

ABSTRACT

When a fish population has been depleted by heavy exploitation, with the yield from the population maintaining an unfavourable level, it is usual to expect that the situation will be improved by reduction of fishing effort. Following a sudden reduction of fishing mortality, p, from p_1 to p_2 at time $\tau = 0$, the yield at once decreases and then increases gradually until it reaches another steady level higher than the former level.

The present paper deals, using Baranov's model, with the transition stage of the population following a sudden change in p, as well as with the steady state before and after the change. Relations between equilibrium yield and fishing mortality rate (effort-yield curves) are calculated for various values of the parameters, λ_0 ($= l_0/u$, where l_0 is the length of a recruit and u is the yearly increase in length), q (natural mortality rate), and b (remaining life span of a fish at the time of recruitment) (Fig. 2). It is noteworthy that for species that grow slowly after recruitment, i.e. when λ_0 is large, reduction of fishing would have scarcely any effect on the yield (Fig. 4).

Yield curves for the period of transition from the present to various lower levels of fishing are calculated for the case in which $\lambda_0 = 4$, $q = 0.15$, $b = 10$ and $p_1 = 1.35$. These represent parameters for the present state of the stock of sohachi flounders *Cleisthenes herzensteini* (Schmidt), in the southwestern area of the Japan Sea (Fig. 5).

Possible density effects on growth rate and natural mortality rate, which are briefly discussed, appear to diminish considerably the effectiveness of any reduction in fishing effort (Fig. 6).

INTRODUCTION

To say that resource problems are necessarily connected with the problem of overfishing is not an exaggeration. And the problem of overfishing frequently brings up the problem of decreasing the number of fishing vessels. Decreasing the number of fishing vessels not only requires many sacrifices but it often produces some unexpected and undesirable effects, so it is not to be lightly adopted as a method of establishing a resource policy. Nevertheless, it is a fact that there are some cases in which it appears that effort is wasted by excessive fishing, and moreover, if left alone, it may exert a destructive influence upon the stock. In such a case, some restrictive measures must be applied to the fishing in order to exploit the fish stock permanently and efficiently. Hence it is necessary to predict the future changes in the size of the stock and in the amount of yield which would result from the restriction of fishing.

There have been many publications over the years concerning the problem of restriction of fishing. Among those which treat the problem mathematically, there is a study by Baranov [1] and by Tauti [7] concerning length restriction

[1]Translated by Hack Chin Kim, United States Bureau of Commercial Fisheries, Seattle; edited by S. Tanaka and W. E. Ricker. The Japanese text of this paper was published in the Bulletin of the Japanese Society of Scientific Fisheries, Vol. 20, No. 7, pp. 599–603, 1954.

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[minimum size limits], and recently Yamanaka [9] has examined the temporal changes in size of a stock after restriction has been imposed, using Baranov's postulates.

In the same article, Baranov also discussed the situation in which fishing effort is reduced, but he considered [page 600] only the equilibrium condition.

Beverton [2] also has presented such concepts as the eumetric yield curve and the optimum fishing intensity, by combining restrictions on body-length and fishing effort.

The purpose of reducing fishing effort is to restore a stock that has been diminished by overfishing and to make possible a greater yield. From the administrative point of view, however, how the stock increases and how the yield changes just after the reduction has been imposed may be more serious matters than the state which will be reached ultimately. For that purpose the theories of Baranov or Beverton are insufficient, since they treat only the equilibrium condition; and it is necessary to find out about the process of change, as Yamanaka has done.

This study follows Baranov's model and includes some numerical computations, together with a simple expansion of the concept into temporal changes. Hence, several of the hypotheses used by Baranov are used here in their original form. These hypotheses contain, as Graham [3] has pointed out, unrealistic elements, and it is to be hoped that these will be remedied by future researches.

My cordial thanks are due to Mr S. Kurita, scientist at the Tokai Regional Fisheries Research Laboratory, who gave me kind instruction in various ways throughout my study of this subject, and to Mr I. Yamanaka, scientist at the Japan Sea Regional Fisheries Research Laboratory who was kind enough to lend me the table of his "yield function".

STOCK SIZE AND YIELD EQUATIONS

Let us assume that a stock which gets a fixed amount of recruitment $N\mathrm{d}t$ between times t and $t + \mathrm{d}t$ has remained in an equilibrium condition for a considerable period of time, being subject to [an instantaneous] fishing mortality coefficient p_1, natural mortality coefficient q, and consequently total mortality coefficient $p_1 + q = i_1$. We assume further (following Baranov) that, after recruitment has occurred, length increases linearly with time τ, and that the fish's body weight is directly proportional to the cube of its length. If length and weight be represented respectively by:

$$l = l_0 + u\,(\tau - t); \qquad wl^3 \tag{1}$$

and the life span of the fish is b, then the total weight of the stock W_1 becomes:

$$W_1 = \int_{\tau-b}^{\tau} w\,[l_0 + u\,(\tau - t)]^3\,\mathrm{N}e^{-i_1(\tau-t)}\,\mathrm{d}t$$

Here when we set:

$$\frac{l_0}{u} + \tau - t = \lambda, \qquad \frac{l_0}{u} = \lambda_0$$

we get:

$$W_1 = wNu^3 \int_{\lambda_0}^{\lambda_0+b} \lambda^3 e^{-i_1(\lambda-\lambda_0)} d\lambda \tag{2}$$

If we use Yamanaka's [9] yield function:

$$\Omega(x, y) = \int_y^\infty y^3 e^{-xy} dy = e^{-xy} \frac{y^2}{x} \left\{1 + \frac{3}{xy} + \frac{6}{(xy)^2} + \frac{6}{(xy)^3}\right\}$$

equation (2) may be expressed as:

$$W_1 = wNu^3 e^{i_1 \lambda_0} \{\Omega(i_1, \lambda_0) - \Omega(i_1, \lambda_0 + b)\} \tag{3}$$

This is the weight of the stock represented by the curve AB in Fig. 1.

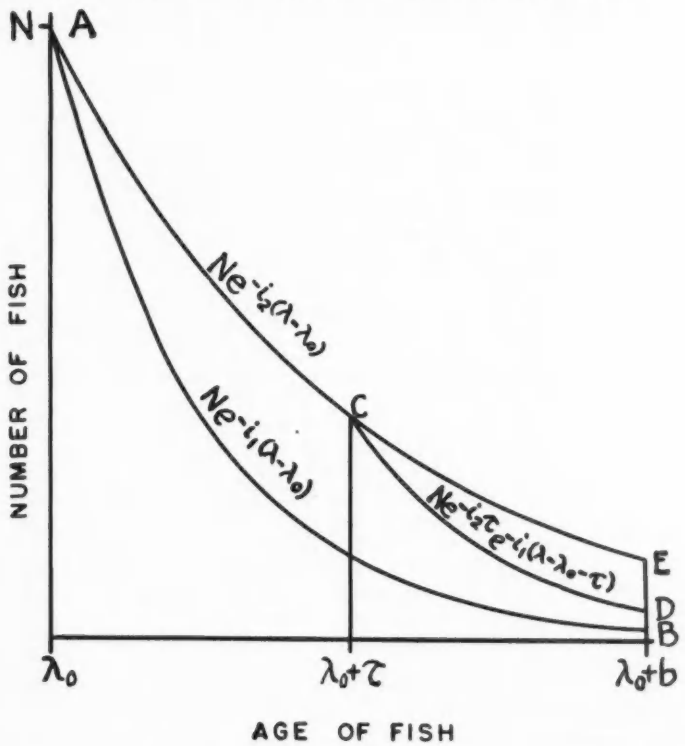

FIG. 1. Curves of mortality. AB: during the period when $\tau<0$. ACD: during the period when $0 \leqq \tau < b$. ACE: during the period when $b \leqq \tau$.

Suppose now with $\tau = 0$ that suddenly p_1 is decreased to p_2 and consequently i_1 is decreased to i_2, the stock at a particular time τ ($<b$) subsequently will be in a state represented by the curve ACD in Fig. 1; and proceeding in the same manner as equation (3) was derived, the size of the stock is obtained as:

$$W(\tau) = wNu^3 [e^{i_2 \lambda_1} \{\Omega(i_2, \lambda_0) - \Omega(i_2, \lambda_0 + \tau)\} + e^{(i_1 - i_2)\tau + i_1 \lambda_0} \{\Omega(i_1, \lambda_0 + \tau) - \Omega(i_1, \lambda_0 + b)\}] \tag{4}$$

[page 601] Further when, with the lapse of time, $\tau = b$, the high-level equilibrium state indicated by the curve ACE in Fig. 1 is reached, and the size of the stock may be expressed by an equation identical with (3):

$$W_2 = wNu^3 e^{i_2\lambda_0} \{\Omega(i_2, \lambda_0) - \Omega(i_2, \lambda_0 + b)\} \quad (5)$$

The yields from the stable conditions before and after the reduction of fishing effort are:

$$Y_1 = p_1W_1, \qquad Y_2 = p_2W_2 \quad (6)$$

respectively; and for the transition period where $0 < \tau < b$, we have:

$$Y(\tau) = p_2W(\tau) \quad (7)$$

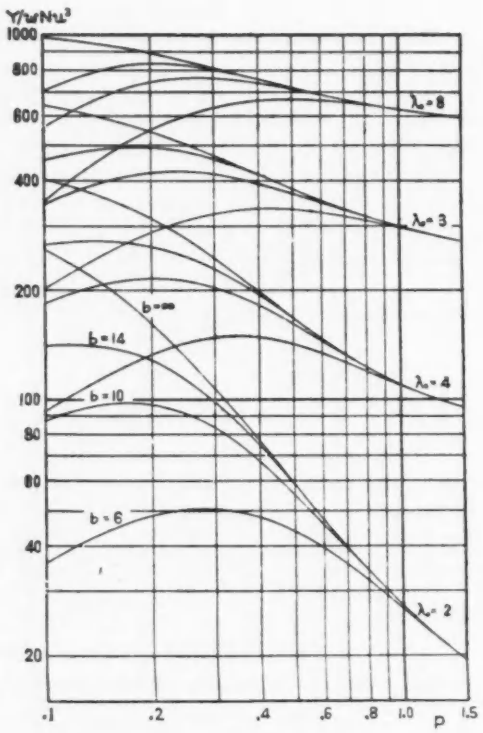

FIG. 2. Curves of yield against effort (rate of fishing, p) when the natural mortality q is 0.15. $\lambda_0 = l_0/u_0$ where l_0 is the length of a recruit and u is yearly increase in length. b is the potential number of years of life remaining to a fish at the time of recruitment.

RELATIONSHIP BETWEEN FISHING EFFORT AND YIELD

Concerning the relationship between fishing mortality coefficient (considered to be directly proportional to the amount of effort) and the yield in a steady state, computations have already been made by Baranov [1] where $l_0 = 30$ cm and $b = \infty$. The same is shown in Fig. 2 for several values of the parameters. According to equations (6) and (3) or (5), the parameters which determine the yield in a steady state are four, namely, p, q, λ_0 and b. In Fig. 2, values of Y/wNu^3 are shown for p-values from 0.1 to 1.5, when $\lambda_0 = 2$, [page 602] 4, 6 and 8, and $b = 6$, 10, 14 and ∞. All these curves were computed for $q = 0.15$, but curves for other values of q may easily be obtained by shifting the p by $(0.15 - q)$ along a straight line which forms a 45° angle with the p axis, as shown in Fig. 3.

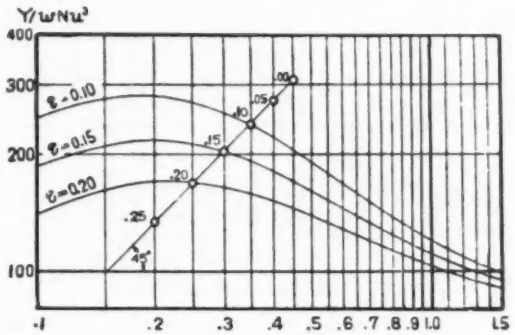

FIG. 3. Curves of yield against effort (rate of fishing, p) for various natural mortality rates when $\lambda_0 = 4$ and $b = 10$. The straight line across the curves shows a method of transforming the curve corresponding to a particular value of q to another, on log-log paper.

As is clear from Fig. 2, there exists a p which can maximize the yield, for certain values of the set (λ_0, b, q). If the actual value of p is greater than this value of p, the yield may be expected to increase if fishing effort is reduced. However, as the value of λ_0 becomes greater (and this means that growth after recruitment is poor), the increase in yield becomes quite small in comparison with the decrease in fishing effort, and this means that restriction of fishing effort is not very effective. Values of Y_2/Y_1 when $p_1 = 1.0$ and $p_2 = 0.5$ are shown in Fig. 4.

THE EXAMPLE OF THE SOHACHI FLOUNDER, *CLEISTHENES HERZENSTEINI* (SCHMIDT)

According to Ouchi [6] and Watanabe [8], sohachi flounders caught in the southwestern part of the Japan Sea become almost completely vulnerable to the fishery when they are one year old, and their length at that time is approximately 12 cm. Their subsequent growth is almost linear, the annual increase

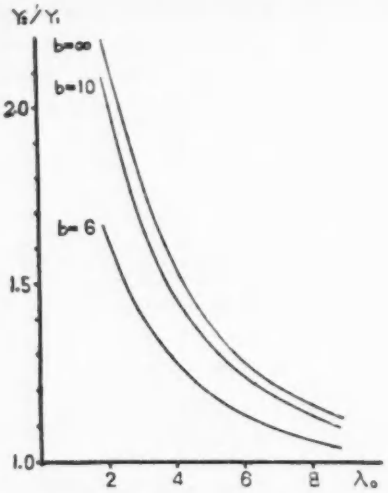

FIG. 4. Increase in yield when fishing mortality p is decreased from 1.0 to 0.5, as calculated from Fig. 2. Observe that as λ_0 becomes greater the increase in yield following decrease in fishing effort is greatly reduced.

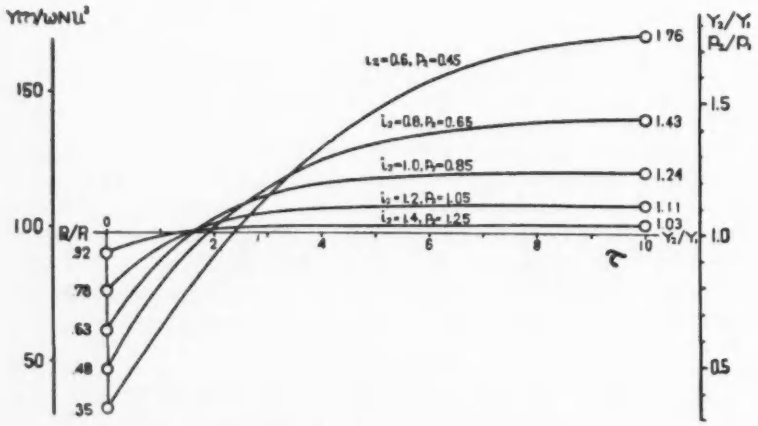

FIG. 5. Curves showing the course of the change in yield after a sudden change of fishing mortality from p_1 to p_2, for a sohachi flounder stock. The horizontal line represents the level of yield before the change (when fishing mortality was equal to $p_1 = 1.35$, and total mortality was $i_1 = 1.50$). The time scale τ, is in years; year 0 is the first year of change from the old to the new rate of fishing.

in length being about 3 cm. The annual percentage survival, obtained from the age composition, is 0.2–0.25; which, when converted into the total mortality coefficient i, becomes 1.6–1.4. On the other hand, according to research by the Hokkaido Regional Fisheries Research Laboratory [4], groups having up to 10 annuli (10 years of age) are encountered.

Figure 5 shows how the yield changes when p_1 is decreased to p_2, when it is given (on the basis of the above data) that $i_1 = 1.5$, $\lambda_0 = 4$, $b = 10$, $q = 0.15$ and consequently $p_1 = 1.35$. The Figure also shows the values of p_2/p_1 and Y_2/Y_1. Even when the effort is decreased by more than half, after about 2 years the yield surpasses the original level, and after 4 to 5 years the temporary loss in yield caused by reduction of effort can be recovered. But subsequent increase in the yield is not very large, and in order to secure as little as 24% increase at equilibrium, effort must be decreased by as much as 37%. Consequently, when the yearly fluctuations in the yield owing to other causes are considered, it may be said that a 10% or 20% decrease in fishing effort has scarcely any substantial effect upon the yield, though it is true that expenses are cut down when the effort is decreased.

EXAMINATION OF THE CHANGES IN NATURAL MORTALITY COEFFICIENT AND GROWTH CAUSED BY INCREASE IN DENSITY

When fishing is restricted and a stock has increased, it may naturally be expected that the natural mortality coefficient should rise and the growth of the individuals should be poor owing to the increased density. All these con-

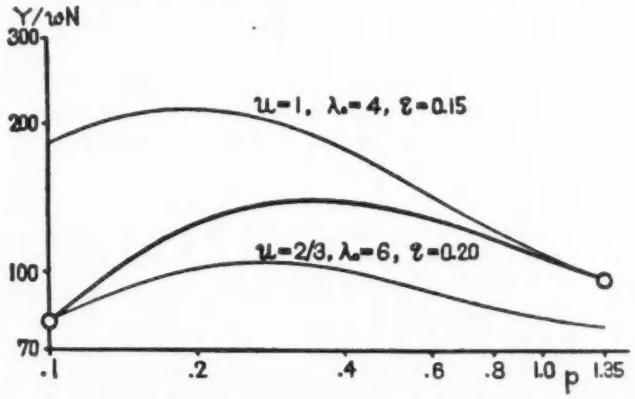

FIG. 6. A hypothetical curve of yield against effort (rate of fishing, p) for a fish population which is subjected to a density effect. The upper and lower curves are ordinary effort-yield curves as in Fig. 2, corresponding to two different sets of conditions for growth rate and natural mortality rate. If the fish population is known to be subjected to one set of conditions (upper curve) at $p = 1.35$ and the other set (lower curve) at $p = 0.1$, an effort-yield curve such as indicated by the middle line in the figure may be computed (for equilibrium conditions at each level of p).

tribute to the weakening of the effect of limitation of fishing, so they should not be ignored. Miller [5], for example, has reported (though it concerns small lakes) that in whitefish fisheries the average body weight increased in spite of the decrease in average age when the fishing effort was suddenly increased. But it is not easy to express these effects in terms of mathematical formulae, and to avoid the danger of making useless or unrealistic assumptions, [page 603] in the foregoing sections growth and natural mortality have been assumed to be invariable. Here let us consider this question somewhat further.

Let us suppose, in the case of the sohachi flounder stock, that the growth rate at $p = 0.1$ is 2/3 of what it is at the present level of $p = 1.35$, and suppose further that q becomes 0.20, instead of 0.15. Then the actual relationship between p and Y in the stock would be something like what is shown by the thick [middle] line in Fig. 6. The ratio of stock densities between these two extremes is 11:1. The numerical values used here for the density effect are all merely hypothetical, but it is easy to see that density effects could considerably diminish the effectiveness of a reduction of fishing.

SUMMARY

1. The relationship between the fishing mortality coefficient p and the yield Y is examined using Baranov's model. Within the range of values of these parameters commonly encountered, the increase in Y which accompanies a decrease in p is not very great. Among species whose growth after recruitment is poor (λ_0 is large), the increase in Y is scarcely detectable.

2. The changes in yield after a reduction in effort has been imposed are calculated for the stock of sohachi flounders in the Japan Sea. If the reduction of effort is less than 50% the yield reaches its former level within 1 or 2 years, and in 2 to 4 years the initial loss resulting from the reduction can be recovered.

But not much increase can be expected in the total yield, though a considerable increase may be expected in yield per unit effort.

3. The ramifications of the effect of density are considered. Using hypothetical numerical values, I have computed the relationship between p and Y in a stock where an effect of density manifests itself [by decreasing growth rate and increasing natural mortality rate]. The density effect weakens considerably the effect of a reduction in fishing.

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Comparison of Ocean Growth and Mortality of Sockeye Salmon During Their Last Two Years[1]

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ABSTRACT

Average instantaneous rates of growth in weight of sockeye (*Oncorhynchus nerka*) of two stocks are computed for their last two growth-years, from scale measurements by Barnaby and Foerster. Values from 0.081 to 0.156 per month are obtained. These rates greatly exceed a *maximum* estimate of instantaneous natural mortality rate, 0.038 per month, for the same period. The latter is based on the total rate of ocean mortality of large smolts, divided by the number of months they are at sea. On this basis, oceanic capture of sockeye during the year prior to their maturation yields less than 35% to 50% of the catch that would be taken from the same fish by a shore fishery the following year. Minimum estimates of loss from high-seas capture of major growth types of sockeye during the year of their maturation vary from 6% to nearly 40%, depending on how early in the season the fishing is done and the particular stock involved. While an increase in mortality rate as sockeye approach shore cannot be excluded, any resulting decrease in the estimate of loss among currently-maturing fish must be accompanied by an increase in the estimate of loss from capture in the year before maturity. In any event, a high-seas fishery that takes any significant fraction of non-maturing sockeye must markedly decrease the total yield from the stocks involved.

INTRODUCTION AND DEFINITIONS

In considering the merits and disadvantages of high-seas fishing as a means of harvesting salmon stocks, its effect on the total yield will be one of the major considerations. This paper compares growth and mortality of sockeye of two stocks during the last two years of their ocean life, and computes the yield obtained by high-seas fishing, in comparison with what a coastal fishery obtains.

Anadromous *life-history types*, or *growth types*, for sockeye are here designated using the Gilbert system. For example, a 6_4 sockeye has 3 complete growing seasons in fresh water and goes to sea at or soon after the start of its 4th growing season (hence the subscript 4); it spends part or all of each of 3 growing seasons in the sea; sexual maturity develops during its 6th year of life; and it lays its eggs just 6 years from the time it began life as a fertilized egg (plus or minus a few days or weeks).

A 6_4 fish is also referred to here as a *3-freshwater* and *3-ocean* sockeye. A great many anadromous life-history types are known, ranging from 2_2 up to 8_5 or so, but only a part of them occur in any one locality. In this paper growth types are grouped according to the length of their ocean life, and rare types are not considered.

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For our purposes the term "ocean life" is taken to include the interval from the time sockeye smolts leave their freshwater nursery lake to the time they appear in coastal or estuarine fisheries on their return journey. For a 3-ocean fish, for example, this interval is here divided into 3 *growth-years*. The growth-years are separated by the scale annuli, the point of division being the outer margin of the closely-spaced circuli or "winter ring". The first ocean growth-year is considered to last from the time smolts leave the nursery lake in spring or summer (hence includes the downriver migration) up to the formation of the first ocean scale annulus the following spring; it is usually or always somewhat shorter than 12 months. The second ocean growth-year extends from the first ocean annulus to the second ocean annulus; it includes a full 12 months, or even a little more if the second annulus is formed later in the season than the first[2]. The last ocean growth-year extends from the time the second ocean annulus is formed to the time the sockeye enter estuarine waters; it is much less than 12 months long, and for some fish it may last as little as one or two months.

GROWTH OF SOCKEYE IN THE OCEAN

Growth During the Penultimate Ocean Season

Computations of growth rate during the period of ocean life have been made for Cultus Lake sockeye maturing in 1925–27, and for Karluk Lake sockeye maturing in 1931 (Appendix I). While Appendix Tables A–C include a variety of growth types, we will be concerned mainly with the dominant types—4_2 at Cultus, 5_3 and 6_4 at Karluk—since these contribute the great bulk of the commercial catch taken from their respective stocks.

These three growth types, shown in Table B, are all 3-ocean fish. Growth made between the time of the scale's first ocean annulus and its second (and last) ocean annulus is assumed to represent 12 months of ocean growth. Computed weights at these two annuli are shown in Table I, columns 3 and 4. Weight increases per month average from 8.4% to 12.8%.

Growth During the Final Ocean Season

Growth of 3-ocean fish in their final season is estimated in Table II. The length of the last growth-year (from the last ocean annulus to the time of near approach to a river) varies greatly between stocks and between individuals. The time the annulus is formed will be discussed later (p. 543). Taking April 1 as the best available estimate of it, the final growth-year for Foerster's Cultus Lake samples lasted about 4.8 months. The Karluk samples of 3-ocean fish were taken June 10, so had had only about 2.3 months of growth in the final year. The percentage increases per month (10.5–16.9%) are about as large as or larger than the 12-month averages for the same fish in the previous year (Table I), mainly because in the final year only months of rapid growth are included.

[2]In several freshwater fishes it has been found that average time of annulus formation becomes later as the fish grow older; however, these fish mature and spawn each spring or summer.

TABLE I. Rate of growth of 3-ocean sockeye in their second ocean growth year (the interval between the two outer scale annuli). Data from Appendix I (Table B and text). Column (7) is the exponential of (6), minus 1.

1	2	3	4	5	6	7
		Weight at ocean annulus formation		Instantaneous growth rate		
Type	Year	First	Second	Total	Per month	Average increase in weight per month
		grams	*grams*			%
Cultus 4_2	1925	336	1309	1.361	0.1134	12.0
Cultus 4_2	1926	428	1380	1.172	0.0977	10.3
Cultus 4_2	1927	298	1256	1.439	0.1199	12.7
Karluk 5_3	1931	332	1172	1.262	0.1051	11.1
Karluk 6_4	1931	486	1288	0.974	0.0812	8.4

TABLE II. Rate of growth of 3-ocean sockeye in their final growth-year. Data from Appendix Table B and the text. Computations as in Table I, but the total instantaneous growth rate (column 6) is divided by the number of months shown in column (3).

1	2	3	4	5	6	7	8
					Instantaneous growth rate		
Type of fish	Year	Growing season	Weight at last annulus	Weight when taken	Total	Per month	Average increase in weight per month
		months	*grams*	*grams*			%
Cultus 4_2	1925	4.8	1309	2133	0.488	0.1017	10.7
Cultus 4_2	1926	4.8	1380	2223	0.477	0.0994	10.5
Cultus 4_2	1927	4.8	1256	2084	0.507	0.1057	11.1
Karluk 5_3	1931	2.3	1172	1679	0.359	0.1562	16.9
Karluk 6_4	1931	2.3	1288	1702	0.279	0.1213	12.9

NATURAL MORTALITY OF SOCKEYE IN THE OCEAN

MORTALITY PERIOD AND STOCKS USED

"Ocean life", as the term is used here for convenience, includes the interval from the departure of the smolts from their nursery lake up to the time they are captured by coastal or river fisheries or return to the spawning river. Thus the estimates of "ocean" mortality include mortality during downstream migration, and also mortality during the upstream migration among such fish as escape the fishery.

Estimates of total mortality are available for the ocean life of the Karluk, Cultus, Babine, Dalnee, Chilko and Bare Lake sockeye stocks (Table III). Data concerning the first four are discussed individually in Appendices II–V. For the Fraser River's *Chilko* stock, lengths are given in table 5 of Clutter and Whitesel (1956), survival rates were computed from the 3_2, 4_2 and 5_2 returns estimated in table 26 of Henry (1961), divided by the estimated numbers of 1-

freshwater smolts in his table 20; and time at sea is based on a comparison of Henry's table 17 with figures 37 and 38 of Clutter and Whitesel. Whereas Chilko Lake has a major commercial stock, the sockeye of *Bare Lake*, Kodiak Island, amount to only 1000 or so adults each year (Nelson, 1959). Average smolt sizes and survival rates (based on estimated catch plus counted escapement) for the counted smolt runs of 1950–53 are given in Nelson's table 8. Average time at sea is estimated on the basis that the average time of smolt departure from the lake and average time of arrival of the adults in the fishery are both about June 15 (table 2, fig. 7); also that there were about 23% 3-ocean adults and 77% 4-ocean adults, on the average, during the years concerned (table 4).

Most of the estimates quoted here were made before high-seas net fishing was started on any considerable scale (Karluk, most of Cultus), or else they apply to stocks which are remote from the region of high-seas fishing and so are probably only negligibly affected by it (Chilko, Cultus, Babine). The Bare Lake sockeye return to western Kodiak Island (154° W Longitude) so early in the season (average June 15) that pelagic capture during the year of their maturity by

TABLE III. Estimates of average ocean mortality among sockeye from 6 localities. (Dalnee figures include some of the fishing mortality; the others exclude all fishing mortality.) Data mostly from Appendixes II–V; figures in column (5) are from Tables F, G, K and L.

1	2	3	4	5	6	7
Lake and smolt years	Av. smolt length	Av. time at sea	Total mortality	Instantaneous mortality rate		Average mortality per month
				Total	Monthly	
	mm	*months*	%			%
KARLUK						
1926–33	143[a]	28	65.8	1.07	0.0382	3.7
1926–33	132[b]	32	72.6	1.30	0.0407	4.0
CULTUS						
1930–31	99[c]	28	92.72	2.62	0.0935	8.9
BABINE						
1955–58	82[c]	30	95.12	3.02	0.1007	9.6
CHILKO						
1951–55	76[d]	27	91.02	2.41	0.0893	8.5
BARE						
1950–53	82[c]	33	95.02	3.00	0.0909	8.7
DALNEE						
1937–40	115[d]	31	63.6	1.01	0.0323	3.2
1938–40, 45	155[b]	27	68.3	1.15	0.0426	4.2
1946	117[d]	31	95.5	3.10	0.1000	9.5
1946–47, 49	161[b]	27	86.7	2.02	0.0748	7.3

[a] 3 freshwater growing seasons.
[b] 2 freshwater growing seasons.
[c] Mostly 1 freshwater growing season.
[d] 1 freshwater growing season.
[e] 1-freshwater and 2-freshwater smolts, in very variable proportions, averaging about 50:50.

TABLE IV. Estimates of average escapement, total stock and ocean mortality among Cultus Lake sockeye of two smolt sizes, as percentages of the number of smolts; and derived mortality rates. Data from figure 4 of Foerster (1954) and Appendix Table B.

1	2	3	4	5	6	7
Av. smolt length	Calculated escapement	Catch plus escape-ment	Ocean mortality	Instantaneous mortality rate		Average mortality per month
				Total	Monthly	
mm	%	%	%			%
63	0.438	1.20	98.80	4.43	0.158	14.7
107	5.395	14.74	85.26	1.915	0.0683	6.6

vessels west of 175° W would be very unlikely. Some Bare Lake fish may well be taken pelagically during their second-last growth-year, but it is unlikely that any large fraction of the stock is found so far west. Thus we can confidently assign the great bulk of the mortality estimated for Bare Lake sockeye to natural causes. The Dalnee sockeye go to sea near the general region where pelagic fishing has been carried on. The smolt years 1937 through 1940 in Table IL might have been affected by it, though the pre-war Japanese pelagic fishing effort was much less than the level attained during the 1950's. In any event, the Dalnee mortality estimates (unlike all the others used) include removals by the coastal fishery as well as any high-seas fishing, and are used here with this reservation (Fig. 1).

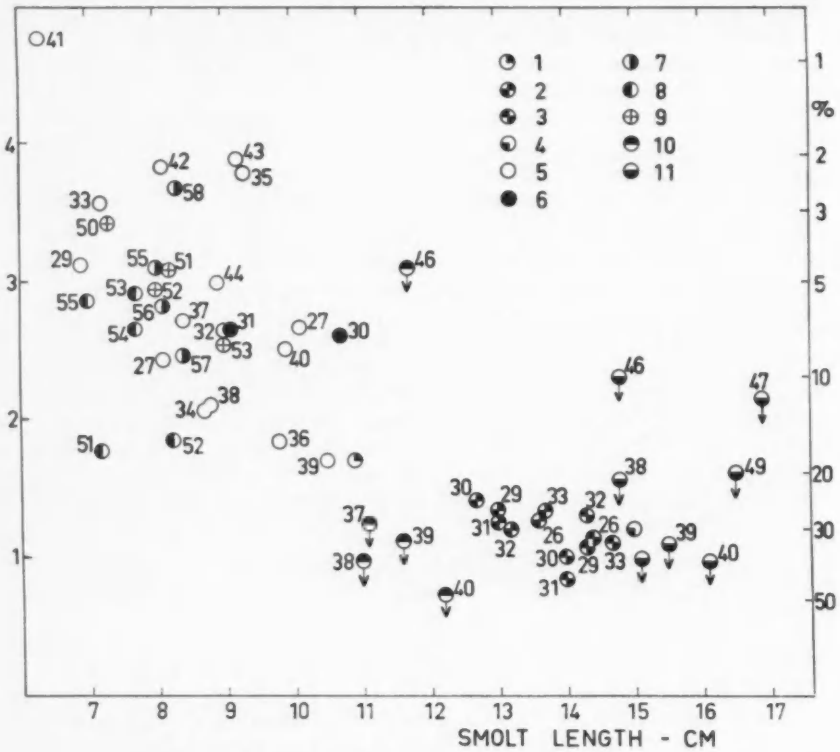
AVERAGE MORTALITY RATES DURING OCEAN LIFE

The figures tabulated in column (5) of Table III are averages of the instantaneous mortality rates for the years shown; columns (4), (6) and (7) are derived from (5). The average number of months at large varies partly because of differences in the dates of downstream migration and of adult return, but the principal variable is the relative number of adults in the 3-ocean and 4-ocean categories, respectively.

Average total losses at sea vary from 95% to 64%, or 3.2% to 9.6% per month. In general, mortality decreases as the size of the smolts increases (Fig. 1), though the Chilko smolts are estimated to have suffered somewhat less natural ocean mortality than the mostly larger Babine, Cultus and Bare Lake smolts.

DISTRIBUTION OF MORTALITY DURING OCEAN LIFE

On general grounds it seems likely that mortality should be greater while salmon are small than it is when they become larger. Table III is consistent with this view, since the smaller smolts had the larger total mortality rates. For example, there is a difference of 1.95 between the instantaneous mortality rates for the Babine smolts (82 mm) and Karluk 3-freshwater smolts (143 mm); this corresponds to 86% actual mortality. If the years concerned are typical (and several years' data are included in each item) this can be taken as a first estimate of the loss which occurs while young Babine sockeye grow from 82 mm to 143 mm—a length increase which is accomplished in considerably less than a year.



1—Karluk (1-freshwater smolts, 1926–33 average);
2—Karluk (2-freshwater smolts); 3—Karluk (3-freshwater smolts);
4—Karluk (4-freshwater smo'ts, 1926–33 average);
5 and 6—Cultus; 7—Babine; 8—Chilko; 9—Bare Lake;
10—Dalnee (1-freshwater smolts); 11—Dalnee (2-freshwater smolts).

FIG. 1. Estimates of instantaneous ocean mortality rates (left-hand scale) for sockeye of 6 stocks. Corresponding percentage survival rates are shown at right. The year beside each point is the year of the smolt migration. The points for Karluk sockeye include an adjustment for mark mortality (see Table G). The clear points for Cultus Lake are based on percentage return to the lake as spawning escapement (Foerster, 1954, table I) multiplied by the average factor 2.73 to adjust them to terms of total stock; the two black points are based on a complete enumeration of returning marked fish in the fishery and at the lake, adjusted for mark mortality (Table F). Dalnee figures (Table L) include some fishing mortality; the arrow pointing downward indicates that these points are all too high to be directly comparable with the rest. All other points represent natural mortality only (including mortality during downstream migration, and that during the upstream migration of fish which escaped the fishery), except that Bare Lake points may include a small amount of high-seas fishing mortality. For other data sources see Appendices II–V, and page 533 of the text.

(The average size of Babine sockeye at the first ocean annulus is not less than 250 mm.) The rest of the ocean mortality must then be distributed over the remaining 2 years or so, and must take 66% of the survivors (instantaneous rate = 1.07).

A somewhat similar comparison of survival rates from smolts of different sizes has already been made by Foerster (1954) at a single locality, Cultus Lake. This comparison has the advantage of the more uniform conditions prevailing within a single stock. Disadvantages are that it pertains to a smaller range of smolt sizes, and that it does not include the catch, so that year-to-year variations in the catch:escapement ratio introduce extra variability into the survival percentages. Column 2 of Table IV compares the computed survival rates corresponding to the largest and the smallest average smolt lengths actually observed at Cultus Lake, calculated from the average relationship of Foerster's figure 4. In column 3 the escapements are both multiplied by the factor 2.73 from Appendix Table D, to make them approximately equal to the combination escapement-plus-catch, and the other columns follow directly.

Between 63-mm smolts and 107-mm smolts there is an increase in survival estimate from 1.2% to 14.7%. Most or all of this difference must represent extra mortality during the early part of the first year of ocean life (including downstream migration), because by the end of their first growth-year in the sea Cultus fish of this type average at least 275 mm long, and even the smallest smolt will have grown well past 107 mm. Thus the intra-stock comparison of Table IV confirms the evidence of the inter-stock comparison of Table III, that most ocean mortality occurs early in ocean life.

Mortality During the Second and Later Years of Ocean Life

We are particularly interested in the ocean mortality after the first ocean annulus is put down—after the sockeye are 25 to 35 cm long. The most straightforward estimate available is the average ocean natural mortality rate for the largest smolts available, which are the Karluk 3-freshwater type (Table III). How typical is their mortality rate of 1.07, corresponding to 34% survival at sea? Apart from their 2-freshwater and 4-freshwater brothers, among North American stocks they can be compared only with smolts of much smaller size, the Cultus, Chilko, Babine and Bare Lake data entered on Fig. 1. The average times at large are not exactly the same for all the points in this figure, and even if they were, it need not be assumed that smolts of a given size necessarily have exactly the same marine mortality in all regions. Nevertheless, the points plotted have a well-defined trend toward less mortality as length increases, and the Karluk groups fit well into the general picture.

To find smolts of size comparable to those of Karluk it is necessary to go to Kamchatka. Mortality estimates for Lake Dalnee smolts are plotted in Fig. 1, from data of Appendix V. There are 7 groups of 2-freshwater smolts and 5 groups of 1-freshwater. (Both types exceed all known American stocks in rate of freshwater growth.) Unfortunately the ocean mortality estimates for these smolts include some fishing mortality, so all the points lie somewhat too high to

be directly comparable with the American figures. Also, the large ocean mortalities of the smolt years 1946–49 are regarded as quite atypical (Appendix V). Even without making any allowance for the last-mentioned, it is clear that the Dalnee observations support the general magnitude of the mortality rates estimated for Karluk smolts of comparable size. If anything, the Dalnee mortalities, when freed of their fishing component, would probably average somewhat less than those for Karluk. Thus available comparisons suggest that the Karluk smolts experienced about average mortality for their size.

It is likely, of course, that even the Karluk smolts experience a somewhat greater mortality rate during the early part of their ocean life than they do in the later part. However, no attempt is made to allow for this quantitatively in what follows: we merely use the Karluk data to obtain a *maximum* mortality estimate for the last two growth-years in the ocean. The average mortality rate of 3.7% per month is applied to all sockeye after the time the first ocean annulus is laid down. Its bias is in the direction of being *too great*.

COMPARISON OF NATURAL MORTALITY AND GROWTH

Penultimate Growth-year

Table V compares growth rates and estimated maximum mortality rate for 3-ocean fish during their second growth-year in the ocean (1st ocean annulus to 2nd ocean annulus). Growth considerably exceeds the maximum mortality estimate in every instance, so that there is a net increase in bulk of each growth-type of fish during this time. The estimated minimum increases vary from 67% to 138% per year, or 4.4% to 7.5% per month.

Table V. Minimum increase in bulk (growth less natural mortality) of 3-ocean sockeye during their second or penultimate ocean growth-year (the interval between the two outer scale annuli). Data from Tables I and III. Column (5) is the exponential of (4), less 1, and (6) is the exponential of 12 times (4), less 1.

1	2	3	4	5	6
	Instantaneous rates (monthly basis)			Minimum increase in bulk of year-class	
Stock and type	Growth rate	Maximum mortality rate	Difference	Per month	Per year
Cultus 4_2 (av.)	0.1103	0.0382	0.0721	7.5%	138%
Karluk 5_3	0.1052	0.0382	0.0670	6.9%	123%
Karluk 6_4	0.0812	0.0382	0.0430	4.4%	67%

Final Growth-year

Table VI shows the difference between growth rate in the final season and the maximum estimate of natural mortality rate, for 3-ocean fish. Minimum estimates of monthly increase in bulk vary from 6.6% to 12.6%.

TABLE VI. Minimum increase in bulk (growth less natural mortality) of 3-ocean sockeye during their *last* growth-year (from the last annulus to the scale edge). Data from Tables II and III.

1	2	3	4	5	6	7
		Instantaneous rates (monthly basis)			Minimum increase in bulk of year-class	
Stock and type	Interval (*months*)	Growth rate	Maximum mortality rate	Difference	Per month	Total
Cultus 4_2 (av.)	4.8	0.1023	0.0382	0.0641	6.6%	36%
Karluk 5_3	2.3	0.1562	0.0382	0.1180	12.6%	31%
Karluk 6_4	2.3	0.1213	0.0382	0.0831	8.7%	21%

EFFECT OF HIGH-SEAS FISHING ON YIELD

If a coastal fishery exists that is capable of taking the optimum percentage of a sockeye stock, then on the basis of Tables V and VI, *any* removal of fish before the end of their sea life causes a loss of potential catch. How large will this loss be in actual practice?

CAPTURE ON APRIL 1 OF THE YEAR BEFORE MATURITY

Suppose a high-seas fishery catches non-maturing 3-ocean sockeye at the start of their next to last growth-year, on April 1. This means that the weight of fish caught will be less than what *could* be obtained from them, by the difference between growth and mortality from that date to the end of sea life the following year. For Cultus Lake fish that would mature as 4_2's, the period involved is 12 months in the penultimate growth-year and 4.8 months in the final growth-year. The minimum estimate of instantaneous rate of increase in bulk (growth less natural mortality) during this time is, from Tables V and VI:

$$(12 \times 0.0721) + (4.8 \times 0.0641) = 1.173 \qquad \ldots (1)$$

Hence the minimum actual increase in bulk, if the fish were not caught, would be to $e^{1.173} = 3.23$ times the weight of fish actually caught. The high-seas fishery would therefore be obtaining only 1/3.23 = 31% of the potential yield from such fish, as a maximum. As compared with a shore fishery that catches sockeye after growth is complete, more than 69% of the possible catch is wasted by the high-seas fishing.

Corresponding figures for Karluk can be based on 4 months of growth in the final growth-year, i.e. capture on July 31 as an average (Barnaby, 1944, table 19). For the Karluk 5_3 type:

Minimum instantaneous rate of increase = $(12 \times 0.0670) + (4 \times 0.1180) = 1.276$ ...(2)
Minimum potential stock at maturity = $e^{1.276} = 3.59$
Maximum high-seas harvest = 1/3.59 = 28%
Minimum percentage wasted = 100 − 28 = 72%

For the Karluk 6_4 type:

Minimum instantaneous rate of increase = $(12 \times 0.0430) + (4 \times 0.0831) = 0.848$ ...(3)
Minimum potential stock at maturity = $e^{0.848} = 2.33$
Maximum high-seas harvest = 1/2.33 = 43%
Minimum percentage wasted = 100 − 43 = 57%

Capture on July 1 of the Year before Maturity

Most high-seas fishing for sockeye is done later than April 1; July 1 would be a more typical date. In principle, a similar computation can be made for this date, but there is the difficulty of estimating the distribution of growth and mortality *within* the penultimate growth-year. A first approximation would be to regard net increase (growth less natural mortality) as uniform throughout this period. We will here use a second approximation, based on preliminary unpublished information concerning seasonal growth of cohoes in the Strait of Georgia. This approximation is that during December through March instantaneous growth rate decreases so that the net rate of increase in bulk is only half as much per month as during April through November. This means that the growth-year has the equivalent of 10 summer months. Fishing on July 1 would therefore occur after 3 of these 10 had elapsed, so the fish taken would have 7/10 of the increase of their penultimate growth-year still before them. Hence to convert to a July 1 capture date it is only necessary to multiply the first term of each of expressions (1)–(3) by 0.7, and continue the computations as before. Results are as follows:

	Cultus 4_2	Karluk 5_3	Karluk 6_4
Minimum instantaneous rate of increase	0.913	1.035	0.694
Minimum potential stock at maturity	2.49	2.82	2.00
Maximum portion of potential yield utilized, when fishing is done on the high seas	40%	35%	50%
Minimum waste by the high-seas fishery	60%	65%	50%

Thus it is clear that catching sockeye during the year before they mature involves a major loss of product.

Capture of Sockeye on the High Seas during Their Final Growth-year

In the year of their maturity, the effect of removal of sockeye by high-seas fishing depends principally upon the length of the time remaining in which growth would have been made if the fish had not been caught. For different high-seas fishing dates, and the different dates that sockeye reach the coast, this can vary from about 1 month to about 4 months. Table VII gives figures for

Table VII. Minimum percentage increases in bulk of a year-class during 1 month and 4 months of the final growth-year, from the data of Table VI; and the corresponding minimum losses if the fish are captured on the high seas 1 month and 4 months before reaching shore.
[% loss = % increase/(100 + % increase)]

	Minimum increase in bulk		Minimum loss of yield	
	1 month	4 months	1 month	4 months
Cultus 4_2	6.6%	29.2%	6.2%	22.6%
Karluk 5_3	12.6%	60.3%	11.2%	37.6%
Karluk 6_4	8.7%	39.4%	8.0%	28.3%

these two periods of time, for 3-ocean fish. Minimum losses from high-seas capture are estimated as 6 to 11% of the possible catch for 1 month, and 23 to 38% of the possible for 4 months. Such losses are less than those suffered when immature fish are captured, but they are quite substantial.

Effect of Change in Natural Mortality Rate near Maturity

It is of course possible that the changed distribution or changed habits of salmon during the last month or two of life might make their natural mortality rate become greater even than the average maximum figure we have been using (3.7% per month). Equally, perhaps, mortality might decrease during this period. For example, capture of salmon by harbour seals and sea lions may well increase as they move inshore, but at the same time they are leaving behind them the much more numerous fur seals.

Whether there is actually an increase in natural mortality rate during the last few months of life and, if so, whether it exceeds the growth made during the same period, must be made a subject for special study whenever a suitable technique can be developed. Here we need only notice that insofar as mortality may become greater during the last month or two, it must then be less than what we have estimated in earlier months (since the total is fixed). Hence if it were to prove necessary to reduce our estimates of loss from high-seas capture of maturing sockeye, we must at the same time increase the estimates of loss suffered by catching non-maturing sockeye.

OTHER LIFE-HISTORY TYPES

Two-ocean Sockeye ("Jacks")

Appendix Table A shows the growth of jack sockeye at Karluk and at Cultus. The Cultus 3_2 figures are a little too low to be representative, because both sexes are given equal weight, whereas jack sockeye at Cultus, as elsewhere, are principally males (90% or more).

Regardless of how many years of freshwater growth they have, 2-ocean sockeye would be apt to be caught by a high-seas fishery only in their last growth-year. The average instantaneous rate of growth of the Cultus jacks during that time was 0.204 per month, twice that of 3-ocean sockeye in their last growth-year (column 3 of Table VI), and the estimate of net increase (growth less natural mortality) is 0.166 per month, 2.5 times that for the 4_2 fish in their last growth-year (0.0641—column 5 of Table VI). From calculations similar to those in Table VII, the minimum percentage loss from early capture of this type of fish in its last growth-year would be 15% for capture 1 month before growth ceases, and 48% for 4 months.

The Karluk jacks were taken at the end of August, much later than the sample of older sockeye there. Their instantaneous rate of growth per month was 0.195 for 4_3's and 0.176 for 5_4's, substantially greater than for either 3-ocean type (column 3 of Table VI). For the 4_3's and 5_4's, respectively, the net loss from high-seas fishing can be estimated as 14% and 13% for 1 month's premature capture, and 47% and 42% for 4 months'.

Although 2-ocean sockeye would suffer a greater *percentage* loss from high-seas capture in the final growth-year than 3-ocean fish would, their small size and scarcity makes this a minor component of the total loss picture.

Three-Ocean Sockeye

The abundant types of 3-ocean sockeye have already been considered, but in Appendix Table B there remain the Cultus 5_3 fish. At Cultus this type was only a small part of the 4-year average sockeye production, although in years when a small run followed a big run the 5_3 fish were an important fraction of *that year's* catch and spawners. The 5_3 sockeye are recruited from a part of their year-class that made slower than average growth in fresh water, and this tendency to slow growth continued throughout the sea life of the group in Table B. The loss from catching these fish on the high seas would be about 30% less than for the 4_2 fish of the same stock, but their scarcity makes them of small importance.

Four-Ocean Sockeye

Appendix Table C presents data concerning the growth of 5_2 and 6_3 sockeye of the two stocks considered. Though these samples are very small, Foerster's (MS) larger samples taken in 1932–33 confirm the fact that 4-ocean sockeye increase in length more slowly than 3-ocean fish of the same freshwater age in every year of life at sea; their instantaneous rates of increase in weight are also less. Consequently estimates of the loss of yield suffered by high-seas capture become less than for the corresponding periods of the other life-history types. If the data for Karluk 6_3 sockeye be taken at face value, these fish practically did not grow at all after their final annulus, and high-seas capture in the final growth-year would have *increased* the yield by about 4% if they were taken 1 month before they reached shore, or by 16% if it were 4 months. For the Cultus 6_3 fish it is about a stand-off between growth and mortality in the final year, while 5_2 fish make a minimum net increase in bulk of about 2% per month, hence there would be a small loss from high-seas capture.

However, this applies only to capture in the final year. If caught in the year before maturity, substantial losses in yield are suffered by all three 4-ocean types, though these are less than those computed for 3-ocean fish on pages 539–540. In addition, 4-ocean sockeye are large enough to be taken on the high seas in the *third* growth-year preceding maturity, and the loss of yield if taken at that time would be much greater than if taken later.

On the whole, the yield from 4-ocean sockeye is likely to be reduced by high-seas fishing about as much as that from 3-ocean sockeye. In most regions 4-ocean fish are not a very large component of the commercial catch. However, several important British Columbia sockeye stocks have a substantial representation of 5_2 fish, and estimation of the balance of growth and mortality for them is under way. It is already evident that for them there is no near-cessation of growth in the final year such as is suggested in Table C for the Karluk 4-ocean sockeye.

DISCUSSION OF SOURCES OF ERROR

Reliability of Calculated Growths

The identification and interpretation of annuli on sockeye scales, particularly the ocean annuli, has presented no great difficulty since the time of Dr C. H. Gilbert's classic studies. The relation of scale radius to fish length has had less attention. Barnaby's empirical curve (Appendix I) is presumably satisfactory for back-calculation of growth of the Karluk fish. The proportionality calculation used for the Cultus Lake fish may be less exact. If the Cultus 3-ocean sockeye conformed to Barnaby's relationship, their computed size at the first ocean annulus would be about 40 mm less, and at the second ocean annulus about 20 mm less, than the values actually used. This increases the estimates of average instantaneous growth rate in the last two growth-years to 0.133 and 0.126, as compared with 0.1103 and 0.1023 in Tables V and VI. The corresponding estimate of loss from a high-seas fishery operating on July 1 of the penultimate year becomes 70%, instead of the 60% on page 540. However, it is not certain that all sockeye stocks will exhibit as curved a body-scale relationship as that obtained at Karluk, and if the computation by Fraser's method errs, it is on the side of conservatism from the present point of view (too small an estimate of high-seas fishing losses).

Representativeness of the Growth Rates of the Stocks Used

The growth rates of the Cultus Lake and Karluk sockeye used here are not likely to be exactly representative of sockeye generally; or rather, each sockeye stock has its own average growth rate and pattern of ages at maturity. On this point, observe that the Cultus 4_2 sockeye of 1925–27 were smaller, as adults, than 4_2 representatives of the major sockeye stocks of the Fraser River. Thus their rate of sea growth was probably a little slower than average for the Fraser, and the estimated loss from high-seas fishing is therefore likely to be a little less than what is typical for this river system.

The Karluk sockeye used by Barnaby were also rather small fish—smaller than Cultus fish of the same types (Appendix Tables A–C). However, the Karluk 3-ocean and 4-ocean types were taken early in the season (June 10), so are small partly on that account: for example, the 5_3 fish would have grown another 30% if they had lived to July 31, at the rate estimated in Table VI, and this would make them 2.2 kg. This is about equal to the Cultus fish, but apparently still a little less than average for Karluk, while the abundant Bristol Bay stocks are usually larger yet. It might be that Barnaby's samples consisted mainly of females, since these tend to have better scales for reading ages.

We conclude that the growth rates used above for Cultus and Karluk fish are somewhat less than average for their respective general regions, hence the estimated loss from catching them on the high seas is somewhat lower than for many sockeye runs.

Time of Formation of Scale Annuli

The average time of formation of ocean annuli is not known with any precision. It may well vary from year to year, in response to sea conditions. The

April 1 date used above was originally estimated from the fact that the ocean (at 50°N, 145°W) *begins* to warm up at about the middle of March, on the average (Meikle, 1961, fig. 3), so that if the beginning of the formation of broadly-spaced circuli depended on increasing temperature it could scarcely occur before the end of that month. On the other hand, Barnaby's 3-ocean sockeye taken on June 10 had put on considerable growth past the last annulus, so that new growth could not have begun much later than April 1 without making the final year's growth rate unreasonably large[3].

The April 1 date, if not the above reasoning, is supported by the observations of Birman (1960), who examined scales from sockeye taken south of the Aleutian Islands in "April" of 1959. He found that some had not completed the annulus, though most of them had "one or more" sclerites of new growth. This is consistent with an average time of annulus formation close to April 1. However, Birman also concluded that pink and coho salmon formed the annulus considerably earlier than sockeye, while chums formed it somewhat later. Thus there is no fixed relationship of annulus formation to temperature or season for Pacific salmon as a whole, and it seems quite likely that there should be differences between different stocks of each species, and between different life-history types within a single stock.

Little improvement in accuracy will be possible until individual stocks and growth types are studied from this point of view. If it should prove, for example, that the annulus for our fish was laid down about March 1 instead of April 1, the final season's average instantaneous growth rate for Cultus 4_2 fish is reduced to 0.085 per month, Karluk 5_2's have 0.112, and the 6_4's 0.085 (compare Table II, column 7). This in turn reduces the estimates of minimum loss from final-year high-seas fishing to 5–7% if one month's growth is lost, and to 20–25% if 4 months' are lost. Corresponding ranges in Table VII are 6–11% and 23–38%, for the 3 growth types. Thus the exact time of annulus formation is not a critical matter.

Estimates of loss from capture of *immature* sockeye at sea are very little affected by shifts in the time the annuli are formed.

End of Growth in the Final Year

The time at which growth ceases in the final year should be studied further. I have assumed growth continues up to the time the fish get close to fresh water, because sockeye stomachs taken in inside waters are often full of food. It is possible, of course, that growth may slow down during the later stages of the marine phase of the spawning migration. However, this would require little change in the estimates of loss from high seas fishing, because our estimates of monthly growth rate in the final year would then be too low. In any event, there cannot be any very large effect of this sort, otherwise the Karluk 3-ocean sockeye

[3]The nine 4-ocean (6_3) sockeye captured on June 10 had grown very little or not at all since the spring annulus, according to Barnaby's interpretation (Table C). Seven of them showed no current-year's growth, that is, the annulus was considered to be at the scale edge. It would be desirable to check this point with new material; if it is typical, then it suggests that the annulus may be formed later among 4-ocean fish than among 3-ocean fish of the same total age. Compare footnote (2), page 532.

taken June 10 could not have put on the substantial growth they did during the short time following annulus formation (Table II, last two lines).

Effect of the Adjustment for Marking Mortality

To obtain an estimate of ocean mortality of Karluk sockeye, the observed ocean mortality rate for marked smolts was divided by 1.27—a figure obtained from experiments at Cultus Lake (Appendix III). What would be the effect on the computations if this adjustment were too great, or too small?

(a) One extreme possibility is to use no adjustment at all. In that event the instantaneous mortality rate of 3-freshwater smolts becomes 1.36 for 28 months, or 0.0486 per month. This figure, instead of 0.0382, is then to be applied in the computations of Tables V–VII. The monthly instantaneous rates of increase in bulk become 0.0617, 0.0566 and 0.0326 for the 3 growth types of Table V, instead of the values shown in column (4) of that Table; and in Table VI the column (5) figures become 0.0537, 0.1076 and 0.0727.

As an example, let us apply these reduced figures in the calculation of expression (1), for Cultus 4_2 sockeye. The minimum estimate of instantaneous rate of increase in bulk during the last two growth-years is:

$$(12 \times 0.0617) + (4.8 \times 0.0537) = 0.998 \qquad \ldots (4)$$

The exponential of this is 2.713, so that the minimum loss from high-seas capture on April 1 of the year before maturity becomes $1 - (1/2.713) = 63\%$—as compared with 69% computed on page 539. Similar results are obtained from the other loss calculations.

(b) Alternatively, we can examine the effect of *increasing* the adjustment for marking mortality. There is no theoretical upper limit that this adjustment can have, but we may try the figure 1.33 obtained for Babine Lake sockeye (Appendix IV). Using this figure, the minimum estimate of monthly instantaneous mortality rate becomes, from Table G, $1.36/1.33 \times 28 = 0.0365$. Using this in column (3) of Table V and column (4) of Table VI, for Cultus 4_2 fish the monthly instantaneous rate of increase in bulk then becomes 0.0738 for the penultimate growth year and 0.0658 for the final growth year. The computation corresponding to (1) and (4) is:

$$(12 \times 0.0738) + (4.8 \times 0.0658) = 1.202 \qquad \ldots (5)$$

Given exponential(1.202) = 3.33, the minimum loss from high-seas capture on April 1 of the year before maturity becomes $1 - (1/3.33) = 70\%$—as compared with 69% estimated on page 539.

Summarizing, it is obvious that the exact size of the correction used for the differential mortality of marked Karluk smolts is not important in this context. Even omitting it altogether makes no very great difference to the estimates of loss from high-seas fishing.

Distribution of Mortality within the Period of Ocean Life

The question of distribution of mortality during ocean life remains a thorny one, not susceptible to direct observation by methods used so far, though it is under study (Parker, 1962). The estimate applied here to the second-last and last growth-years is the average monthly mortality rate of Karluk 3-freshwater

smolts during the whole time they were at large. This estimate has two weaknesses. For one thing, it may be too great to represent the purely oceanic mortality of stocks which are already well out to sea by the time they average 143 mm long. The Karluk smolts of this size still had to pass through coastal waters before getting out into pelagic conditions. In addition, it seems reasonable to suppose that ocean mortality rate should decrease a bit throughout life as the size of the fish increases, whereas we have assumed a constant instantaneous rate after 143 mm is reached. Both of these circumstances tend to make the Karluk mortality estimate too great for our purpose, since we are here dealing only with the penultimate and final growth-years in the ocean, not the first growth-year. Consequently the ocean mortality figure used, 0.0382 monthly on an instantaneous basis or 3.7% per month, has been considered a maximum estimate, not a best estimate. The true value might, for example, fall as low as 2% per month, or perhaps even 1%, toward the end of ocean life. Parker (1962) estimates an average figure $q = 0.32$ for instantaneous per annum ocean mortality rate (excluding coastal mortality); this amounts to 0.0267 per month, as compared with 0.0382 used here.

Any reduction in the mortality estimate below 0.0382 would increase estimates of the potential yield lost by high-seas fishing, but of course not proportionally. For example, if the instantaneous natural mortality rate used in Tables V and VI be cut in half, to 0.0191 per month, the increase in bulk (growth less natural mortality) of the Karluk 5_3 fish in their penultimate growth-year becomes 181% instead of 123% (cf. Table V); while the yield from such fish caught on July 1 of their penultimate year becomes:

$$\frac{1}{\exp\left[(0.7 \times 12 \times 0.0861) + (4 \times 0.1371)\right]} = \frac{1}{3.57} = 28\% \qquad \ldots (6)$$

of the possible yield. Thus the loss from high-seas capture of this type of fish at this time would become 72% of the possible catch, as compared with the minimum figure 65% computed on page 540.

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Dr M. P. Shepard and Mr J. McDonald have supplied the data concerning Babine sockeye used in Table K, while Dr R. E. Foerster made available his supplementary observations on the growth of the Cultus fish and supplied references to other pertinent information. These and other members of the staff of the Nanaimo Station of the Fisheries Research Board of Canada have also made many useful suggestions concerning the content of the paper. Dr R. R. Parker is to be specially thanked for recommending that the *ratio* of instantaneous mortality rates be used to adjust for marking mortality.

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APPENDIX I. INCREASE IN WEIGHT OF CULTUS AND KARLUK SOCKEYE AT SEA

In spite of an abundance of age determinations of sockeye, computations of their growth history from scale annuli are scarce. Gilbert (1918) used freshwater growth patterns, mainly, to distinguish different sockeye stocks, but also used sea growth in a few instances; however he did not compute complete growth histories from the scales, nor are these given in Henry's (1961) comprehensive work on the Fraser stocks. Foerster (1929) and Barnaby (MS, 1932) computed rates of growth from sockeye taken in 1926 at Cultus Lake (Fraser system, southern British Columbia) and in 1931 at Karluk Lake (Kodiak Island, Alaska).

Foerster calculated lengths by a variant of the method first used by McLean Fraser (but often called Rosa Lee's method). Scales were measured from the first circulus to successive annuli and to the scale edge; and proportionality was assumed between these measurements and the length of the fish less 1.2 inches (32 mm). In Foerster's table 4 the computed increments are shown; those for the first year do not include the fish length prior to the first circulus, but the length at annulus 1 can be obtained by subtraction of all later increments from the length of fish at capture. In Tables A–C the growth of males and females at Cultus is averaged, giving each sex the same weight. In general, the males grew somewhat faster than the females.

Barnaby used an empirical curve for his back-calculation of length, based on measurements of scales of fingerlings, smolts and adults at Karluk Lake. Using a graph of log scale radius against actual fish length, the scale measurements of each fish were adjusted mechanically (using a pair of dividers) to the average scale size for fish of the observed length, and the length at each annulus was then read off the curve directly. I have used the average values given for each of the 4 growth types in Barnaby's table 2, and have computed lengths similarly for the nine 6_2 fish whose scale measurements are given in his appendix (p. 49). Barnaby does not indicate the sex of the fish he used.

Computed fork lengths at successive annuli, and length at the scale edge, are shown in columns 2 and 5 of Tables A–C, for the various life-history types. The fish go to sea at the time an annulus is formed or soon after, so that (for example) the Karluk 5_3 fish which grew from 126 to 326 mm in their third growing season did this almost entirely in salt water.

In Tables A–C weights are computed from length by means of the relationship:

$$\log W = -1.954 + 2.958 \log L \qquad \ldots (7)$$

Here W is round weight in grams, L is fork length in centimetres. Expression (4) is based on data for Cultus Lake sockeye, as shown in Fig. 2. It is a relationship between average lengths and average weights for samples from whole groups of fish of a particular type—not the weights and lengths of individual fish. Thus the exponent 2.958 is analogous to a "between-ages-*b*" (Ricker, 1958, p. 191), suitable for computing *average* weight from the *average* length of a representative group of fish of a given life-history type.

Each figure in columns 4 and 7 of Tables A–C shows the instantaneous rate of growth up to the annulus it stands opposite, from the previous annulus.

In addition to the 4_2 sockeye of the 1926 run shown in Table B, Dr R. E. Foerster has kindly made available unpublished data on the growth of 17 male and 88 female 4_2 fish of the 1925 run, and 29 males and 141 females of the 1927

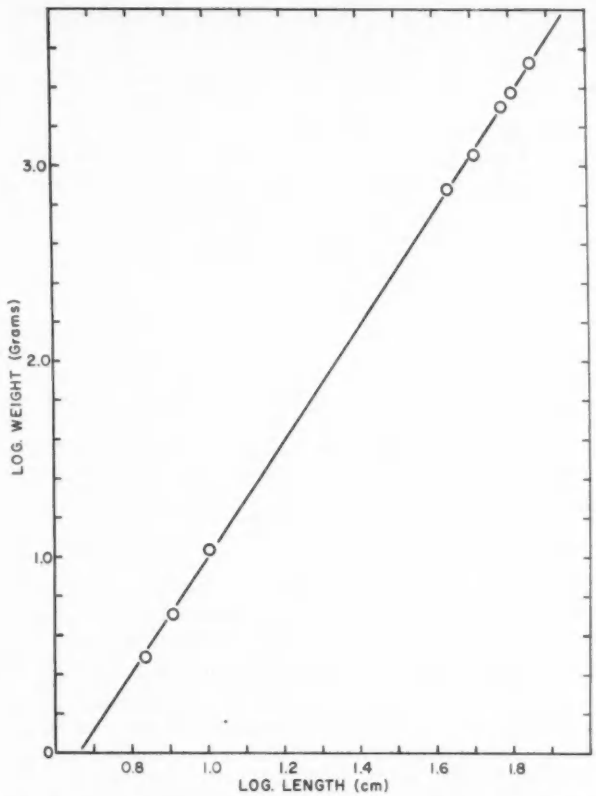

FIG. 2. Relation between logarithm of average weight and logarithm of average fork length for several classes of Cultus sockeye smolts (points at lower left) and adults (points in upper right).

run[4]. Average calculated lengths at successive annuli for the two sexes (giving equal weight to each) were 102, 327, 518 and 611 mm for 1925, and 79, 314, 511 and 606 mm for 1927. Treating these as in Table B, the successive instantaneous rates of growth in weight become 3.447, 1.361 and 0.488 for the 1925 fish, and 4.082, 1.439 and 0.507 for 1927. The 1927 run was in the "dominant" sockeye line at Cultus Lake at that period, and was much more numerous than 1925 or 1926, or indeed both of these together. Ocean growth of the 1927 fish was the

[4]Foerster (MS) has also computed the increments for a variety of growth-types of Cultus *marked* sockeye taken in 1932 and 1933 in the commercial fishery. These data are not used here because of the possibility that the marks used (removal of both ventral fins, or of both ventrals and the adipose fin) might have affected growth rate. Actually, however, the computed increments for the 4_2 fish of 1932 and 1933 are very similar to the figures for 1925 and 1927. The 4_2 fish of the small 1926 sample (Table B) were considerably larger than any of the others at the first ocean annulus, but this superiority was much reduced at the last annulus and at the time of capture.

most rapid of the three years, at least part of the reason being that although they were only about half as large (in weight) when they left fresh water, this deficiency was almost wholly made up during their ocean existence. There would be some justification for using the 1927 year-class as the most representative one for the calculations of this paper, but in order to embrace as broad a set of ocean conditions as possible, simple averages of the instantaneous growth rates for the three calendar years available are used in the text above: these averages are 1.324 for the penultimate growth-year and 0.491 for the final growth-year.

The average dates of the seaward and return migrations of these fish are approximately as follows:

Migrants leave for sea:
- Cultus—April 25
- Karluk—June 5

Adult growth ceases:
- Cultus—August 25 (Samples were taken at the lake, mostly in October, but growth ceases earlier, at the time the fish approach fresh water.)
- Karluk 4_2 and 5_4—August 31 (Samples were taken in the coastal fishery on that date.)
- Karluk 5_3, 6_4 and 6_5—June 10 (Samples were taken in the coastal fishery on that date.)

The dates shown for the Karluk adults are those on which the samples happened to be taken, *not* the average time of return for the respective life-history types.

TABLE A. Growth of 2-ocean sockeye ("jacks") of the Karluk and Cultus stocks. Samples at Karluk were taken August 31, 1931; those at Cultus in autumn, 1926. Average fork length in millimetres (L), weight in grams (W) and instantaneous growth rates (g) between successive annuli are shown. Average weight is computed from the length using expression (4) of the text. Each instantaneous growth rate is the difference of the natural logarithms of the weight adjacent to it and the one just above it. The first year of ocean growth is marked by an asterisk (*). Note that the growth-year from the last annulus to the scale edge is less than a calendar year. Data from Foerster (1929) and Barnaby (MS, 1932); see the text for details.

1	2	3	4	5	6	7
	Karluk			Cultus		
Annulus	L	W	(g)	L	W	(g)
				GROWTH TYPE 3_2 (53♂, 24♀)		
1	...	...	...	85	6.22	...
2	...	...	...	351	413.	4.195*
edge	...	...	...	489	1102.	0.981
	GROWTH TYPE 4_3 (7 FISH)			GROWTH TYPE 4_3 (1♀)		
1	69	3.38	...	76	4.48	...
2	127	20.51	1.803	139	26.73	1.789
3	370	483.1	3.159*	387	552.	3.034*
edge	514	1279.	0.974	546	1531.	1.022
	GROWTH TYPE 5_4 (33 FISH)					
1	57	1.914	...			
2	104	11.32	1.778			
3	142	28.44	0.921			
4	381	528.	2.922*			
edge	513	1271.	0.878			

TABLE B. Growth of 3-ocean sockeye of the Karluk and Cultus stocks. Samples at Karluk were taken June 10, 1931; those at Cultus in autumn, 1926. For explanation see Table A. See page 549 for additional Cultus 4_2 specimens.

1	2	3	4	5	6	7
	Karluk			Cultus		
Annulus	L	W	g	L	W	g
				GROWTH TYPE 4_2 (4♂, 36♀)		
1	...	...	...	100	10.09	...
2	...	...	...	355	427.6	3.746*
3	...	...	...	527	1380.	1.172
edge	...	...	...	620	2223.	0.477
	GROWTH TYPE 5_3 (22 FISH)			GROWTH TYPE 5_3 (4♂, 12♀)		
1	67	3.08	...	72	3.82	...
2	126	19.95	1.867	133	23.44	1.814
3	326	332.	2.811*	373	495.4	3.051*
4	499	1172.	1.262	546	1531.	1.128
edge	564	1679.	0.359	615	2178.	0.352
	GROWTH TYPE 6_4 (17 FISH)					
1	68	3.24	...			
2	106	11.97	1.308			
3	151	34.2	1.050			
4	371	486.	2.655*			
5	515	1288.	0.974			
edge	566	1702.	0.279			

TABLE C. Growth of 4-ocean sockeye of the Karluk and Cultus stocks. Samples at Karluk were taken June 10, 1931; those at Cultus in autumn, 1926. For explanation see Table A.

1	2	3	4	5	6	7
	Karluk			Cultus		
Annulus	L	W	g	L	W	g
				GROWTH TYPE 5_2 (1♂, 2♀)		
1	...	...	...	105	11.67	...
2	...	...	...	294	244.9	3.044*
3	...	...	...	432	765.6	1.140
4	...	...	...	538	1466.	0.649
edge	...	...	...	590	1928.	0.274
	GROWTH TYPE 6_3 (9 FISH)			GROWTH TYPE 6_3 (2♂, 1♀)		
1	75	4.32	..	72	3.82	...
2	122	18.20	1.442	128	20.94	1.705
3	324	326.6	2.894*	362	453.9	3.082*
4	462	933.	1.053	522	1340.	1.084
5	619	2218	0.867	603	2051	0.427
edge	620	2228	0.005	641	2460	0.182

APPENDIX II. OCEAN MORTALITY OF CULTUS LAKE SOCKEYE

Mortality among Marked Smolts

Calculations of rate of return (catch + escapement) are given by Foerster (1934, 1936) for the smolt runs of 1930 and 1931. These smolts were marked by removing fins: both ventrals (BV) in 1930, and adipose and both ventrals (AdBV) in 1931. The entire sockeye catch of southern British Columbia and adjacent Washington was searched for these marks in the appropriate years (Table D). In both smolt years the whole migration had been marked, and in the returning years unmarked individuals of the ages in question were negligible in number among the fish that reached the home lake.

Table D. Percentage returns of marked sockeye to Cultus Lake, and computed mortality rates. (Data from Foerster, 1934, 1936.)

1	2	3	4	5	6	7
		Returns of marked fish				
Smolt year	Smolt size	Catch	Escapement	Total	T/E	Instantaneous mortality rate
	mm	%	%	%		
1930	107.0	1.91	1.763	3.67	...	3.31
1931	90.8	2.65	0.865	3.51	...	3.35
Av.	98.9	...	1.314	3.59	2.73	3.33

Comparison of Mortality among Marked and Unmarked Smolts

Previously *a portion* of two smolt migrations had been marked: using AdBV in 1927, and half the dorsal plus BV in 1928. Returns *to the lake only* are shown in Table E.

The instantaneous mortality rates for marked and unmarked smolts can be compared on the basis of their difference or their ratio. The *difference* is appropriate to a situation where most or all of the handicap due to marking is expressed in extra mortality that occurs during a short period of time following marking and is independent of smolt size. The *ratio* is appropriate to a situation where the loss of fins creates a continuing handicap throughout life, increasing the instantaneous mortality rate by a fixed *percentage* in every year.

Table E. Comparison of mortality rates of marked and unmarked smolts at Cultus Lake. (Data from Foerster, 1934, 1936, 1937.)

1	2	3	4	5	6	7	8	9
		Escapement to lake			Instantaneous mortality rates			
Smolt year	Smolt size	Marked	Not marked	Ratio	Marked	Not marked	Difference	Ratio
	mm	%	%					
1927	100.7	0.878	2.486	0.353	4.74	3.69	1.05	1.28
1928	80.8	1.344	3.25	0.414	4.31	3.43	0.88	1.26
Av.	90.8	1.111	...	0.383	...	...	0.96	1.27

Available evidence favours the latter interpretation. Foerster found that marked smolts held for several weeks in ponds at Cultus Lake suffered practically no mortality, while the marking scars healed over completely. Similar results have been obtained for other salmonids of comparable size. On the other hand, the data of Appendix VI show that absence of fins is a serious handicap to adult sockeye in the trying environment of an obstructed river. Being pursued by seals, sharks or halibut in the sea seems likely to be equally trying, and could lead to a differencial in mortality between marked and unmarked salmon of all sizes in salt water that is just as great as that experienced by the smolts. Thus present information favours the view that the *ratios* of the instantaneous rates (column 9 of Table E) are the more appropriate basis for comparison. Parker *et al.* (in press) reached this conclusion regarding pink salmon; they found that the ratios of the instantaneous mortality rates of marked and unmarked were very similar in nature and in experiments where fry were held in a tank with a trout.

TABLE F. Mortality and survival rates of marked Cultus sockeye of the 1930 and 1931 smolt migrations, adjusted by the average ratio of instantaneous mortality rates of marked and unmarked smolts (from Tables D and E).

1	2	3	4
		Adjusted statistics	
Smolt year	Smolt size	Instantaneous mortality rate	Catch plus escapement
	mm		%
1930	107.0	2.60	7.46
1931	90.8	2.64	7.16
Av.	98.9	2.62	...

In the Cultus sockeye experiments, the two ratios of instantaneous mortality rates are practically identical, averaging 1.27 (Table E). On a day-to-day basis, therefore, the marked fish were on the average about 27% more vulnerable to the causes of death in operation[5]. A less direct comparison at Babine Lake gives the figure 33% (Appendix V).

The good agreement of the two Cultus marking mortality ratios justifies using 1.27 to adjust the results of the 1930 and 1931 experiments to the basis of unmarked smolts; particularly (as Foerster points out) since the *absolute* levels of percentage return of marked fish to the lake were much the same for the 1930–31 experiments as for those of 1927–28[6]. The adjusted figures are shown in Table F.

[5]A marked-to-unmarked comparison was made on this basis earlier (Ricker, 1949, p. 30). Dr R. R. Parker points out that because of an error in taking logarithms, the ratio of instantaneous rates for the 1927 smolts was given there as 1.13, instead of the true value 1.28.

[6]The average is 1.11% for 1927-28 (Table E, column 3) and 1.31% for 1930-31 (Table D, column 4). The difference is small in comparison with the difference between marked and unmarked smolts, and it is in the direction expected from the somewhat larger average size of the 1930-31 smolts.

APPENDIX III. OCEAN MORTALITY OF KARLUK LAKE SOCKEYE

Mortality among Marked Smolts

Barnaby (1944) gives details of marking experiments at Karluk Lake, made in 1926 and from 1929 to 1933. The sockeye smolts there are among the largest known in America: at the time of his work they were primarily fish with 2 or 3 freshwater growing seasons, but adult fish from smolts with 0, 1 and 4 freshwater annuli were also observed[7]. Returning fish were predominantly those with 3 ocean growing seasons (including incomplete seasons), although those with 4 ocean seasons were an appreciable fraction of the total, especially among 2-freshwater fish. Various marks were used; the following are used here to estimate survival:

1926:	AdRV, AdLV	1931:	AdBV
1929:	AdBV	1932:	AdRV, AdLV
1930:	AdRV, AdLV	1933:	AdBV

By sampling and "ageing" the smolts marked, Barnaby estimated the number of each age marked as they went to sea; similarly he sampled the marked adults in the catch and determined *their* ages throughout the season; the sample ratios were then applied to the total catch and to the escapement. Average rates of return from the 2- and 3-freshwater smolts were remarkably uniform (Table G). Few 1-freshwater and 4-freshwater smolts were marked, so their percentage returns are much more variable (actual numbers of returns are shown in Barnaby's tables—the smallest number in a year was 1). The average size of each type of smolts was obtained from Barnaby's table 27; although length samples are not available for every week, within-year variation tends to be less than between-year, and the yearly averages for 2- and 3-freshwater smolts must be correct within a millimetre. Percentage survival increased with age and size from 11.6% at 109 mm to 19.3% at 132 mm and 25.5% at 143 mm, and was down slightly to 24.8% at 150 mm.

Adjustment for the Effect of Marking

Unfortunately there is no direct check on marking mortality in the Karluk experiments, because the whole smolt run was not counted. However, the need for some adjustment of the Karluk returns to compensate for a marking handicap is suggested qualitatively by other evidence. In some years additional smolts were marked at Karluk, using the adipose and the pectoral (P) or dorsal (D) fins, and these gave somewhat smaller returns (Table H). If removal of a pectoral fin or the dorsal fin causes an appreciably greater handicap than removing one or even both ventrals, it seems extremely likely that there is also some survival differential between the adipose-plus-ventral marks and no mark at all. Barnaby (1944) was of the same opinion.

[7]Smolts with 2 freshwater growing seasons are here called "2-freshwater", whereas Barnaby calls them "3-freshwater", presumably so as to agree with the subscript in the Gilbert system of designation life-history types.

TABLE G. Average lengths (L) and estimated percentage returns (R), of Karluk smolts marked by removal of the adipose and one or both ventral fins. Data from Barnaby, 1944, tables 27, 31-35, 37, 39, 41. Figures for 1926 do not include 4-ocean returns.

Smolt year	Freshwater growing seasons (annuli)							
	1		2		3		4	
	L	R	L	R	L	R	L	R
	mm	%	mm	%	mm	%	mm	%
1 1926	100	4.9	136	20.0	144	23.7	163	34.2
2 1929	...	...	130	18.3	143	25.5	153	13.5
3 1930	110	2.5	127	16.6	140	28.0	140	32.5
4 1931	111	54.8	130	21.2	140	34.5	144	40.8
5 1932	...	...	132	21.8	143	19.2	152	2.3
6 1933	114	18.8	137	18.3	147	25.9	147	15.6
7 Average[a]	109	11.59	132	19.30	143	25.54	150	24.8
8 Instantaneous mortality	2.16		1.645		1.365		1.39	
9 Adjusted mortality	1.70		1.296		1.074		1.10	
10 Adjusted return	18.3%		27.4%		34.2%		33.3%	

[a]For 2-freshwater and 3-freshwater smolts the average survivals are the geometric means of the survival rates for the 6 years, each year having the same weight. For 1-freshwater and 4-freshwater smolts, the average is the total of the actual returns estimated for all years divided by the total estimated number of smolts marked.

TABLE H. Comparison of ventral, dorsal and pectoral marks on Karluk sockeye, by freshwater ages. Data from Barnaby, 1944, tables 34-42.

1	2	3	4	5	6	7	8	9	10
	Survival rates, as percentage						Instantaneous mortality rates		
1930 *experiment*	AdRV	AdLV	Av.	AdRP			Ventrals	Pectorals	Ratio
2-freshwater	16.9	16.3	16.6	15.2	...	...	1.80	1.88	1.04
3-freshwater	26.8	29.2	28.0	20.8	...	...	1.27	1.57	1.23
1931 *experiment*	AdBV	AdD					Ventrals	Dorsal	Ratio
2-freshwater	21.2	18.0	...	...	...	...	1.55	1.72	1.11
3-freshwater	34.5	30.1	...	...	...	...	1.06	1.20	1.13
1932 *experiment*	AdRV	AdLV	Av.	AdRP	AdLP	Av.	Ventrals	Pectorals	Ratio
2-freshwater	19.1	23.7	21.4	20.7	16.2	18.45	1.54	1.69	1.10
3-freshwater	20.5	17.3	18.9	14.6	12.0	13.3	1.67	2.02	1.21

In the circumstances, the best available procedure is to apply to the Karluk fish the ratio of instantaneous mortality rates for marked and unmarked smolts that was obtained at Cultus Lake (Appendix II). This means dividing the figures in row (8) of Table G by 1.27, to give the adjusted mortality rates of row (9). The corresponding adjusted survival rate, in row (10), is the negative exponential of (9). The adjustment increases the survival rate for 2-freshwater smolts by 42%, and that for 3-freshwater smolts by 34%. The adjusted mortality rates have been computed for each year for the 2- and 3-freshwater smolts and are plotted in Fig. 1, but only the average figure is plotted for the scarce 1-freshwater and 4-freshwater types.

APPENDIX IV. OCEAN MORTALITY OF BABINE LAKE SOCKEYE

Marked Smolts

In 1946–48 about 100,000 smolts leaving Babine Lake (upper Skeena River system) were marked AdBV each year—300,528 in all. In the same 3 years a similar number of smolts leaving Lakelse Lake, tributary to the lower Skeena, were marked BV. During 1947–51 inspection for marked adults was made yearly in the Skeena fishery and as consistently as possible at the Babine River fence. However the fence could not be operated in 1948, and in 1951 a rock slide downstream from the fence necessitated a special estimate of escapement (Table J).

Table J. Returns of sockeye marked in 1946, 1947 and 1948 to the Skeena River fishery and Babine River fence in 1947-1951. (Preliminary data from records of the Fisheries Research Board of Canada's Nanaimo Station—MS Annual Reports for 1947-51; and from Godfrey *et al.*, 1954.)

Year of return	Type	Place	Mark	
			AdBV	BV
			no.	*no.*
1947	2–ocean	Fence	16	0
1948	3–ocean	Fishery	327	...
	2– and 3–ocean	Fence	305[a]	21[b]
1949	3– and 4-ocean	Fishery	345	...
	2–, 3– and 4–ocean	Fence	298	21
1950	3–, 4– and 5–ocean	Fishery	957	...
	3–, 4– and 5–ocean	Fence	693	25
1951	4– and 5–ocean	Fishery	933	...
	4– and 5–ocean	Fence	83	11
	4– and 5–ocean	Blocked by slide	750[c]	52[d]
Totals			4707	130

[a]Estimated by applying, to the estimated escapement, the ratio of AdBV marks to total fish examined in the commercial fishery, and then dividing by 1/0.75 to adjust for the non-Babine fish in the commercial catch.

[b]Estimated as 6.97% of the number of AdBV (6.97 is the geometric mean of the three observed ratios of BV to AdBV).

[c]The total escapement (other than 2-ocean fish) from the commercial fishery was estimated as the fence count, 140,000 (= 92% of 152,457), plus the estimated loss due to the slide (319,000)—see Godfrey *et al.*, 1954. The number of AdBV marks in this escapement was estimated from those in the commercial catch by the procedure described in (a) above, and the 83 AdBV marks actually observed at the fence were subtracted (since they are listed in the previous row).

[d]Estimated as 6.97% of 750; cf. (b) above. The ratio for 1951 alone, 11/83 = 13.3%, is based on few fish and is high in comparison with other years and other experiments.

If we consider BV's at the Babine fence to be mismarked or regenerated AdBV's (that is, assume that all Lakelse BV's went to Lakelse), the estimated accounted-for return is 4837 sockeye from 300,528 marked. To this figure should be added: (1) some small part of the BV's in the commercial fishery; (2) possibly some part of the "doubtful" marks; (3) a small allowance for sockeye caught by Indians below the Babine fence (Skeena only); (4) a very few 5-ocean fish in 1952; (5) a certain number of marked fish missed at the counting fence. These would bring the total to possibly 5200–5500. For the lower of these figures, survival rate is 5200/300,528 = 1.732% and average instantaneous mortality rate is $i = 4.06$; for the larger, survival is 1.831%, and $i = 4.01$. In what follows 4.03 will be used as a best estimate.

Unmarked Smolts

Table K gives preliminary figures for size and survival of unmarked sockeye smolts leaving Babine Lake in recent years. The average lengths, determined from samples, are subject to revision, but they could scarcely be shifted as much as 5 mm in either direction. These data are plotted in Fig. 1.

Table K. Estimated numbers and average fork lengths of Babine downstream migrants, and the adult return produced by them (catch plus escapement). (Preliminary data from Messrs J. McDonald and M. P. Shepard, Fisheries Research Board of Canada, Nanaimo Station.)

Smolt year	Smolts		Adult return	Survival rate	Instantaneous mortality (i)
	Length	Number			
	mm	*millions*	*thousands*	%	
1955	80.1	30.9	1391	4.50	3.10
1956	80.9	21.1	1258	5.97	2.82
1957	83.9	4.5	386	8.57	2.46
1958	83.1	22.2	566	2.55	3.67

Comparison of Marked and Unmarked Smolts

The average of the instantaneous mortality rates in Table K is 3.02, for unmarked smolts of the years 1955–58. The average for the marked smolts of years 1946–48 was 4.03, above. Hence the ratio of mortalities of marked to unmarked is 4.03/3.02 = 1.33. This comparison cannot be exact, because the sizes of smolts marked in 1946–48 might have been somewhat different from those of the runs of 1955–58, and of course ocean mortality rates can vary from year to year. Nevertheless 1.33 is rather close to 1.27, the average ratio estimated by comparing marked and unmarked smolts of the same migrations at Cultus Lake (Table E).

APPENDIX V. OCEAN MORTALITY OF LAKE DALNEE SOCKEYE

The extensive work done on sockeye salmon at Lake Dalnee, Kamchatka, provides data relevant to our problem. Table L is a summary of percentage

returns of a number of smolt groups to the lake and perhaps to Dalniaia River fisheries. Unfortunately catches taken farther downstream and in the sea are not included, but these fish matured during the war and early post-war years when "outside" fishing was not very active, so the known returns probably represent a fairly large fraction of the total.

TABLE L. Estimates of size and survival of Lake Dalnee sockeye of various smolt groups. Data from Krogius and Krokhin (1948) and Krogius (1961). W—weight; L—fork length; R—percentage return to Lake Dalnee and associated fisheries (other fisheries not included); (i)—instantaneous mortality rate for the whole period of absence.

Smolt migration year	1-freshwater smolts				2-freshwater smolts			
	W	L	R	(i)	W	L	R	(i)
	g	*mm*	%		*g*	*mm*	%	
1937	14.7	111	29.0	1.24	42.4	159	...	...
1938	12.8	110	38.0	0.97	31.5	148	21.1	1.56
1939	15.7[a]	116	33.0	1.11	36.5	155	33.5	1.09
1940	17.4	122	48.0	0.73	42.3	161	38.0	0.97
1945	...	...	20.0	1.61	33.8	151	37.0	0.99
1946	16.2	117	4.5	3.10	31.9	148	10.0	2.30
1947	14.5	113	...	...	48.0	169	11.7	2.15
1948	...	...	9.3	2.38	35.6	154	...	...
1949	...	...	...	...	44.5	165	20.0	1.61

[a]Krogius and Krokhin's (1948) table gives this figure as 23.0 g; I have used the more recent figure plotted on Krogius's (1961) graph, for which the corresponding length is 116 mm, and which agrees much better with points for adjacent years (Fig. 1). In all other instances the 1961 graph agrees closely with the data tabulated in 1948 for smolt years 1937-40.

The average lengths and weights of the various smolt groups through 1945 are from table 14 of Krogius and Krokhin (1948); for later runs average weights were read from figure 1 of Krogius (1961) and were converted to length, approximately, using expression (4) of Appendix I. Percentage returns in Table L are from table 3 of Krogius (1951). Average times at sea (given in Table III) are estimated on the basis that average smolt departure is on July 1 and average adult return August 1; also, half of the 1-freshwater smolts and 80% of the 2-freshwater smolts are considered to be 3-ocean fish, the remainder being 4-ocean (cf. Krogius and Krokhin, 1948, tables 18, 19).

There are two unusual features of these results. One is the abrupt drop in ocean survival rate for the smolt years 1946–49, which caused a disastrous decrease in abundance of the Dalnee stock. The same occurred among other east Kamchatka and, to some extent, Alaska sockeye stocks, and it was accompanied by very slow sea growth among at least one of the Dalnee year-classes involved. For want of any alternative, Krogius and Krokhin (1956) are inclined

to blame the whole syndrome on unusual, but unidentified, ocean conditions; they wonder whether the severe earthquakes off the eastern Aleutians in 1946 might not somehow be involved.

The other peculiarity of the Dalnee mortality figures is that during the 1937–40 period of good survival the average mortality rate of the 1-freshwater smolts was somewhat less than that of the 2-freshwater smolts, in spite of the fact that the latter were much larger and spent about 4 months less at sea, on the average. Conceivably a selective fishery might account for this, but that is only a guess. For the 1946–49 smolt years, however, the difference was in the more usual direction: percentage return of 2-freshwater smolts was about double that of 1-freshwater smolts of the same year-classes (1944 and 1946 spawnings).

APPENDIX VI. NATURE OF THE MARKING HANDICAP

When marked smolts are retained in captivity in fresh water for a few weeks following marking, the fin scars commonly heal over quickly, with very little mortality. This has caused some to doubt the reality of a marked:unmarked differential in adult returns. A possible explanation is that the handicap of a missing fin must consist in some loss of speed or maneuvrability at moments when the fish is under unusual strain—for example, when being chased by a predator. Such moments must occur from time to time throughout life, not merely right after marking.

This continuing-handicap hypothesis is supported by events during the Babine sockeye run of 1951. In that year a rock slide on the Babine River, below the counting fence, proved a severe trial to all the fish that reached it: only about a third of the 3-ocean and older sockeye got past, according to the estimates of Godfrey *et al.* (1954, p. 26). The 140,000 sockeye counted at the fence were the survivors of about 459,000 that reached the slide (30.5%). The run that year included the 4-ocean survivors of Babine smolts marked AdBV in 1948, and possibly a very few 5-ocean survivors of smolts similarly marked in 1947. Marks were checked in the fishery (in the sea and on the lower river, far below the slide) and at the fence (above the slide), as follows:

	Fishery	Fence
Examined	685,000	140,000
AdBV marks	933	83
Percentage marks	0.136%	0.059%

The fishery included about 25% non-Babine fish, so its percentage should be increased to allow for this—to approximately 0.136/0.75 = 0.18%. On this basis, the total AdBV marks among the fish that reached the slide was 0.18% of 459,000 = 830. Hence the 30.5% of the Babine sockeye that got past the slide area included only 83/830 = 10.0% of the estimated number of AdBV marks that reached the slide. That is, the absence of these fins reduced the

capacity of the sockeye to pass the difficult spot to 10.0/30.5 = 33% of that of normal sockeye[8].

The corresponding instantaneous mortality rates are 2.30 for the marked fish and 1.19 for the unmarked, ratio 1.93. This may be compared with the average ratio 1.27 for Cultus smolts and 1.33 for Babine smolts, as given earlier. Evidently passage of the obstructed river was a much more demanding and selective situation than the average of all sources of mortality experienced by sockeye during ordinary migrations and ocean life.

[8]A potential complication was avoided by the nature of the blockade and water levels in 1951. From the smolt migrations of 1946–1948 the marked adult sockeye always arrived at the Babine fence at an earlier average date than the unmarked ones, by about 3 weeks. The reason is that the smolts marked were mostly from the later portion of the smolt run, that largely consisted of smolts from the up-lake stocks which as adults return early in the season. This would have been a disturbing complication *if* the passability of the obstruction had varied throughout the summer of 1951. However, Godfrey *et al.* (1954, p. 27) assessed the seasonal obstructiveness of the rock slide in 1951 and concluded that "at no time is there indication of any complete and persistent block; rather, a fairly constant proportion of about one-third of the run escaped daily above the slide".

Estimations of Ocean Mortality Rates for Pacific Salmon *(Oncorhynchus)*[1]

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ABSTRACT

A conceptual model representing natural marine mortality rates of Pacific salmon is developed. Ocean mortality rate (q) is taken as the base to which coastal mortality rates of juveniles (c) and of adults (k) are additive factors. The effect of marking is taken as a multiplicative factor (m) of the instantaneous rate (i) where $i = q + c + k$. Together with time these values are incorporated into the balanced equation

$$c + k = \frac{1}{m}[\mathrm{Ln}N_0 - \mathrm{Ln}(R_1e^{mt_{0.1}q} + R_2e^{mt_{0.2}q} + R_3e^{mt_{0.3}q} + \cdot\ +)]$$

where N_0 denotes the population entering the sea and R_1, R_2, R_3 denote the returns at succeeding times of maturity. The locus of $c + k = f(q)$ is used to graphically depict all possible combinations of $c + k$ and q within the limits $[q, c + k = 0]$. Intersections of loci are taken as estimates of values of q and $c + k$ which satisfy two sets of data. Available data for sockeye salmon (*O. nerka*) from Cultus Lake, Chilko Lake and Hooknose Creek, British Columbia, Karluk River and Bare Lake, Alaska, and Dalnee River, Kamchatka, pink salmon (*O. gorbuscha*) and chum salmon (*O. keta*) from Hooknose Creek, chinook salmon (*O. tshawytscha*) from the coast of Southeast Alaska and coho (*O. kisutch*) from the Eel River, California, are utilized. It is concluded that ocean mortality is relatively constant, of the order of magnitude $q = 0.32$ or $S = 73\%$ annually. A juvenile coastal mortality factor (c) apparently exists and is characteristic of the species and race through the media of size of migrants, time spent in the costal area, and geography. An adult coastal factor (k) may exist but is of negligible influence on the total mortality rate. While the data utilized collectively may be considered as extensive, serious defects in sampling errors and undefined variability were encountered. It is doubted that mortality rates can be more accurately defined from any repetition of experiments used, hence a more direct approach is indicated for solution of this problem.

INTRODUCTION

There are very few published efforts on the estimation of oceanic natural mortality rates of Pacific salmon. Two authors, Barnaby (1944) and Foerster (1936a), presented estimates of catch and escapement resulting from populations of marked sockeye (*Oncorhynchus nerka*) smolts. Krogius and Krokhin (1948) have presented estimates of seaward migrating populations of sockeye smolts and partial catches and escapements attributable to these groups. Escapements attributable to known seaward migrations of pink (*O. gorbuscha*) salmon fry and the escapements resulting from single marked populations of pink and chum (*O. keta*) fry are available from Hunter (1959). Murphy (1952) estimated the survival of coho salmon (*O. kisutch*) during the final 12-month period of life;

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however, his estimates do not separate mortality attributable to fishing from that due to natural causes. Parker and Kirkness (1956) and Parker (1960) estimated the annual rate of survival from natural causes of tagged chinook (*O. tshawytscha*). Henry (1961) estimated marine survival for several brood years of Chilko sockeye (Fraser River, B.C.). Parker (1962) estimated the natural mortality rates of pink and chum salmon, based on data of Hunter (1959) and theoretical arguments arising from the fecundity of these species. Ricker (1962) has discussed ocean mortality rates for sockeye, using some of the above experiments plus data for the Skeena River and for Bare Lake, Kodiak Island (Nelson, 1959). It is surprising that such a short list should exhaust the published data on such an important statistic.

It is the purpose of this communication to assemble these data, together with two unpublished sockeye marking experiments, and interpret the results according to a model for sea mortality. From this comparison the extent and deficiencies of our present knowledge may become known.

A MORTALITY MODEL

Upon entrance into the sea, young of the Pacific salmon are observed in coastal waters for a period of time, the length of period varying with species and geographic location (Clemens, 1952; Foskett, 1951; Manzer, 1956). Sockeye, chum, pink and to a lesser extent coho then move offshore and are found as mixed populations in the oceanic habitat (INPFC, 1960; Neave and Hanavan, 1960; Birman, 1958; Semko, 1958). While chinook salmon may occasionally be found offshore, they are commonly encountered as immature feeding fish in coastal or enclosed waters. To some extent this is true of coho. Upon maturity, however, all species must again proceed into and through the coastal belt.

Vernon (1958) and Wickett (1958) demonstrated significant correlation between the relative success of pink and chum salmon brood years (at maturity) and temperature and salinity observations of coastal waters during the summer months following seaward migration. Henry (1961) has demonstrated a direct correlation between first year marine growth and marine survival. These observations may indicate a rather critical period of variable mortality during early life in the sea followed by a prolonged period of lowered mortality in the ocean. Higher mortality rates may again be encountered when the maturing segments of the populations re-enter the coastal zone. These ideas are symbolically expressed in the following model.

A population of smolts (N) enters the sea at time t_0. At time t_1 the population is reduced by sources of mortality which occurred at the instantaneous rate (i) throughout the time period $t_{0\text{-}1}$, that is:

$$N_0 = N_1 e^{t_{0\text{-}1} i} \tag{1}$$

If, during the initial juvenile period in coastal waters, the mortality rate is different than in the following period in oceanic waters, this difference may be expressed as an additive factor:

$$i = q + c \tag{2}$$

where q denotes the base oceanic rate and c denotes the difference between the oceanic rate and the total rate actually encountered during the initial time period. If prior to t_1 a fraction of the surviving population N_1 matures and re-enters the coastal area, that fraction may be subject to a further change in natural mortality rate. Here k denotes the difference between $q + c$ and i applicable to maturing salmon in the coastal area. Thus where fish enter the sea and mature at the end of a single time period:

$$i_1 = q_1 + c_1 + k_1 \tag{3}$$

When the maturing portion of the stock is subject to fishing mortality during the ultimate year *only*, at the instantaneous rate p:

$$i = q_1 + c_1 + k_1 + p_1 \tag{4}$$

If a portion of the remaining population matures at t_2, for $t_{0\text{-}1}$, $i_1 = q_1 + c_1$ and for $t_{1\text{-}2}$, $i_2 = q_2 + k_2 + p_2$, thus the entire schedule of mortality for that segment of the population is:

$$i_{0\text{-}2} = c_1 + q_1 + q_2 + k_2 + p_2 \tag{5}$$

Similarly, a third fraction of the remainder may mature at t_3 and for that segment of the population:

$$i_{0\text{-}3} = c_1 + q_1 + q_2 + q_3 + k_3 + p_3 \tag{6}$$

and so on. Letting E_t denote the escapement from each maturing segment the balanced equation depicting the population during the total time in the sea takes the form:

$$N_0 = E_1 e^{c_1+q_1+k_1+p_1} + E_2 e^{c_1+q_1+q_2+k_2+p_2} + E_3 e^{c_1+q_1+q_2+q_3+k_3+p_3} + \ldots \tag{7}$$

Assuming (in the absence of data) no differences among the q_t, the k_t or the p_t, equation (7) reduces to:

$$N_0 = E_1 e^{c+q+k+p} + E_2 e^{c+2q+k+p} + E_3 e^{c+3q+k+p} + \ldots \tag{8}$$

When the effects of the fishery are known, the return (R_t) may be estimated as the catch (C_t) plus E_t and:

$$N_0 = R_1 e^{c+q+k} + R_2 e^{c+2q+k} + R_3 e^{c+3q+k} + \ldots \tag{9}$$

Multiplying equation (9) by $e^{-(c+k)}$:

$$N_0 e^{-(c+k)} = R_1 e^{q} + R_2 e^{2q} + R_3 e^{3q} + \ldots \tag{10}$$

Time periods vary for successively maturing segments of the population; thus equation (10) must take the form:

$$N_0 e^{-(c+k)} = R_1 e^{t_{0\text{-}1}q} + R_2 e^{t_{0\text{-}2}q} + R_3 e^{t_{0\text{-}3}q} + \ldots \tag{11}$$

Much of the data available has been obtained through the use of populations of marked individuals. The effect of marking on survival of Pacific salmon has received some study (see Ricker, 1949, 1962; and Parker *et al.*, 1962) resulting in the suggestion that removal of fins causes a significant increase in the instan-

taneous natural mortality rate throughout life. This effect may be expressed as a multiplicative coefficient (m) of the instantaneous rate (i), for the absolute increase is relative to the magnitude of the prevailing mortality rate. From equation (11), the statement depicting natural mortality rates but based on empirical observations of marked fish takes the form:

$$N_0 e^{-m(c+k)} = R_1 e^{mi_{0.1}q} + R_2 e^{mi_{0.2}q} + R_3 e^{mi_{0.3}q} + \ldots \qquad (12)$$

Taking natural logarithms:

$$\begin{aligned} \mathrm{Ln}N_0 - m(c+k) &= \mathrm{Ln}[R_1 e^{mi_{0.1}q} + R_2 e^{mi_{0.2}q} + R_3 e^{mi_{0.3}q} + \ldots] \\ c + k &= \tfrac{1}{m}[\mathrm{Ln}N_0 - \mathrm{Ln}(R_1 e^{mi_{0.1}q} + R_2 e^{mi_{0.2}q} + R_3 e^{mi_{0.3}q} + \ldots)] \end{aligned} \qquad (13)$$

Equation (13) defines $c+k = f(q)$ independent of the numerical values of N_0 for different populations. For each set of empirical data the right-hand term is evaluated for trial values of q and the results plotted as $c+k = f(q)$. The resulting lines depict the locus of $c+k = f(q)$ for any desired range of q and/or $c+k$ (see Fig. 1).

The function has no real meaning at values of $q<0$ as negative values would imply reproduction within the population. Negative values of $c+k$ (where $c+k<q$) imply a coastal mortality rate less than the oceanic mortality rate. While this situation may be possible it is considered improbable, for (a) the density of competing and predatory species diminishes as the salmon leave the coastal waters and (b) the small fry are considered to be more vulnerable to predation than the larger juveniles. In the present treatment only positive values of $c+k$ and q are entertained and the limits $[c+k, q = 0]$ enclose the portion of the locus that is biologically acceptable.

Data for two populations of smolts N_{a0} and N_{b0} may be available with which to form a pair of simultaneous equations, viz., from equation (11):

$$N_{a0} e^{-(c_a+k_a)} = R_{a1} e^{i_{0.1}q_a} + R_{a2} e^{i_{0.2}q_a} + R_{a3} e^{i_{0.3}q_a} + \ldots \qquad (14a)$$

$$N_{b0} e^{-(c_b+k_b)} = R_{b1} e^{i_{0.1}q_b} + R_{b2} e^{i_{0.2}q_b} + R_{b3} e^{i_{0.3}q_b} + \ldots \qquad (14b)$$

If $c_a = c_b$, $k_a = k_b$ and $q_a = q_b$ then equation (14b) can be multiplied by the fraction N_{a0}/N_{b0} and subtracted from equation (14a). The left-hand terms will vanish. *Provided* the ratio of right-hand terms in equation (14a), *e.g.*,

$$R_{a1} e^{i_{0.1}q_a} : R_{a2} e^{i_{0.2}q_a} : R_{a3} e^{i_{0.3}q_a}$$

and so on, is *different* from the ratio of right-hand terms in equation (14b), an equation with one unknown (q) will result.

Similarly, from equation (13) loci of the functions $c_a + k_a = f(q_a)$ and $c_b + k_b = f(q_b)$ may intersect, the point of intersection indicating values of $c+k$ and q which satisfy both sets of data. Loci resulting from equation (13) are equivalent to loci of polynomials of degree maximum t, plotted on a log-log axis. The lines have both slope and curvature depending upon the periods of time between entrance into the sea and maturity, and upon the fraction of the population which matures at each time of maturity. These quantities which govern the shape and slope of the locus are referred to as the "maturity schedule" of the

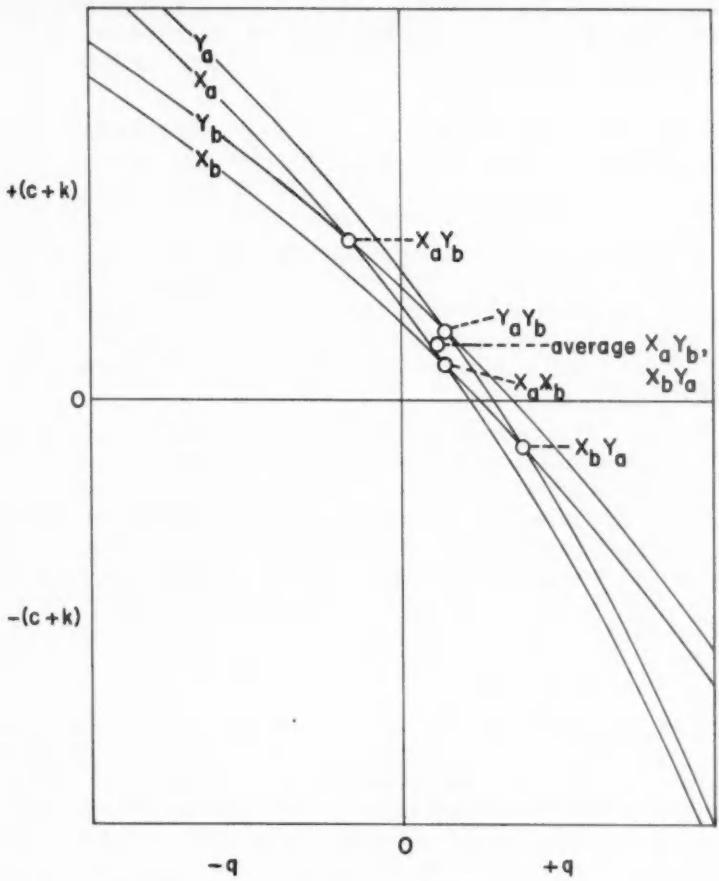

FIG. 1. Hypothetical example of the effect of curvature on average values of q, $c + k$ (a and b with identical maturity schedules).

population. The position of the locus, in respect to the axes, is governed by the mortality rates $c + k$ and q.

For the case where lines representing two populations having different maturity schedules but subject to identical mortality rates intersect, the point of intersection is at the true values of $c + k$ and q. When two populations have identical maturity schedules but different mortality rates, the lines will not intersect (at reasonable values of $c + k$ or q) but will lie nearly parallel to each other, the distance separating them being a measure of the difference in mortality rates. Where two populations have dissimilar maturity schedules and dissimilar

mortality rates, the lines may intersect but the indicated value of $c+k$ is too low and the corresponding value of q too high for the average mortality rates, or vice versa, depending upon which population has the higher (or lower) mortality rates.

No attempt has been made to determine the statistical reliability of these common solutions for paired sets of data. In general the greater the divergence in maturity schedule the greater the angle of intercept and therefore the intercept will lie closer to true average values for a given difference in mortality rates.

Intercepts beyond the limits are common and these clearly indicate that the basic premise of identical mortality rates has been violated. If the loci were straight lines and the data extensive, an average of intercepts would be expected to correctly represent average values of $c + k$ and q. The loci are, in actuality, shallow curves and it is therefore necessary to limit those intersections which may be averaged.

For an example, two groups of migrating smolts, X and Y, may be subdivided into types X_aX_b and Y_aY_b on the basis of age and sex. The X age group generally suffers less mortality[2] than the Y group; however, the a and b sex-divisions have *identical* maturity schedules. This situation is diagrammatically presented as Fig. 1. It is seen that while the intersections X_aX_b and Y_aY_b accurately depict the given situations, an average of the intersections derived from the reciprocal pairs X_aY_b and X_bY_a does not, because of the curvature, lead to the average of X_aX_b and Y_aY_b. The case where a and b have non-identical maturity schedules is depicted in Fig. 2. In this situation the average X_aY_b and X_bY_a becomes displaced below the limit area.

Situations encountered with data reviewed and to be presented in the present paper most closely resemble that depicted in Fig. 2. Small differences in mortality and maturity schedule, either real or arising from sampling error, become grossly magnified in their effect at the higher $\pm q$ values. For these reasons point solutions of $q, c+k$ arising from paired equations, which fall outside the limits [q, $c+k = 0$], are eliminated from further consideration.

The validity of point solutions of $q, c+k$ is *not* established simply because the intersects fall within the limits [q, $c + k = 0$]. However, the *possibility* that the criteria of similar mortality rates and the dissimilar maturity schedules are satisfied *may be entertained*. Within this limited area, and at leavels of q and $c+k$ encountered, distortion due to curvature and to smallness of the differences in maturity schedules (in the case of reciprocal pairs) are minimized. Shifts in intercept are then largely due to differences in mortality rate (either real or due to sampling error, e.g., in the estimates of the numbers marked of each age group of smolts) and an average of these intercepts has some validity as a description of the average situation. These concepts form the basis of the present analysis of sea mortality rates.

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[2]In this example the difference in mortality between X and Y groups has been assigned entirely to a difference in $c + k$. This does not alter the general conclusions.

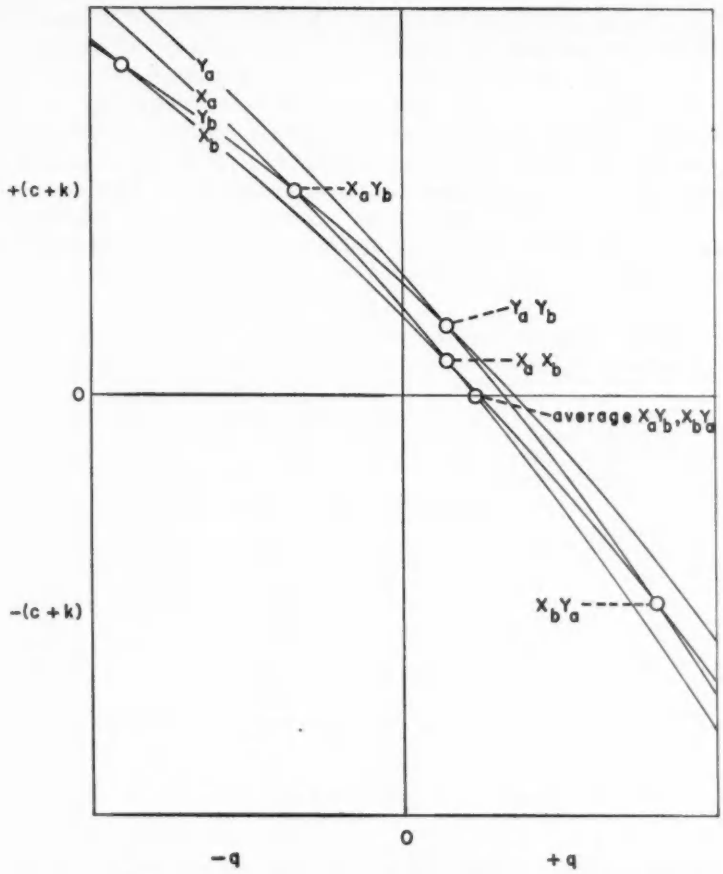

FIG. 2. Hypothetical example of the effect of curvature and non-identical maturity schedules on average values of q, $c + k$.

KARLUK SOCKEYE

Barnaby (1944) reported the results of a series of experiments with Karluk River, Alaska, sockeye. Smolts were captured at the lower extremity of the river, marked by fin amputation, and released. Daily samples were taken from which the age composition of the marked populations was estimated. Catches of returning adults, taken by beach seine in the close proximity of the river, were subsequently sampled to obtain the incidence of marks within any particular age classification. These ratios were then applied to the total runs as estimated by catches of sockeye in the Karluk area and the escapements enumerated at a counting weir to obtain an estimate of adults returning from the marked smolt populations.

For the purposes of the present analysis, the data are restricted to those experiments using adipose and ventral fin removal. In years where the A + RV and A + LV marks were both used the experiments are combined. For the 1930 experiment using A + LV, two mark recoveries were reported for the 2/4 age classification[3] although the sampling programme failed to indicate that fish of that group were present in the returning adult run. From the other marked to unmarked ratios this recovery has been taken to represent 18 fish returning. No other alterations have been made except to correct obvious errors. Data from Barnaby's Tables 33–35, 37, 39, and 41 are summarized and presented here as Table I. Only the 2- and 3-freshwater annuli groups are utilized.

TABLE I. Karluk sockeye data (from Barnaby, 1944, tables 33-35, 37, 39, 41).

Year marked (t_0)	Calculated number marked (N_0)	Calculated returns after 1 yr (R_1)	2 yr (R_2)	3 yr (R_3)	4 yr (R_4)
		Smolts with 2 freshwater annuli			
1929	21,858	656	2882	450	0
1930	29,599	70	3317	1533	18
1931	41,403	39	3845	4857	46
1932	15,656	13	2089	1265	57
1933	25,394	7	3208	1441	0
		Smolts with 3 freshwater annuli			
1929	28,041	1002	5362	783	0
1930	19,327	335	4631	395	0
1931	8,145	119	2349	339	0
1932	14,173	159	1806	718	35
1933	13,692	45	2423	941	0

No data appear available with which to estimate the effect of marking for the Karluk stocks. The experiments of Foerster (1934, 1936a, 1936b) have been reviewed by Ricker (1949, 1962) who suggests that $m = 1.27$ for Cultus sockeye. This figure has been borrowed to apply to the Karluk stock.

From Rounsefell (1958, fig. 43, 44) the average date of arrival of 50% of the maturing population for each life history type has been estimated. Barnaby (1944) estimated the peak of downstream migration for 2-annuli smolts as June 21 and for 3-annuli smolts as June 14. From this information the total time at sea, expressed as decimal fractions of whole years, was calculated for each life history type and is presented in Table II.

With the data summarized in Tables I and II and the value $m = 1.27$, $c+k = f(q)$ was calculated from equation (13). The results are presented in

[3]In this paper, age is designated as freshwater annuli/saltwater annuli. The age classification 2/4 is equivalent to 7_3 of the Gilbert system used by Barnaby (1944) and Foerster (1936a), and to 6_2 of the system used by Krogius and Krokhin (1948).

Table III and loci of the function are graphed in Fig. 3 and 4. In Fig. 3 and 4 the limits [q, $c+k = 0$] are indicated. The curves are shallow and may be taken as linear over short intervals of q.

TABLE II. Estimated average time period (in years) at sea for each life history type of Karluk sockeye. Data from Rounsefell (1958) and Barnaby (1944). The sea "year" is taken from time of smolt migration.

Freshwater annuli	Sea annuli			
	1	2	3	4
2	1.19	2.08	2.97	3.96
3	1.23	2.19	3.00	4.00[a]

[a] Rounsefell does not provide data for this estimate; however the value 4.00 cannot be far from correct.

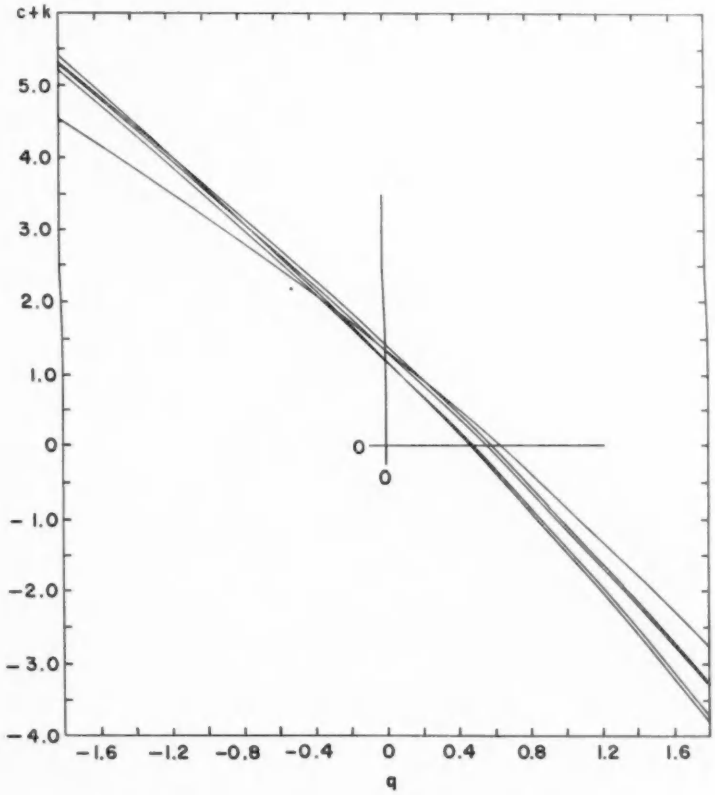

FIG. 3. Loci of $c + k = f(q)$, Karluk 2-annuli sockeye smolts.

TABLE III. Values of $c + k = f(q)$, Karluk sockeye.

q	2-annuli smolts					3-annuli smolts				
	1929	1930	1931	1932	1933	1929	1930	1931	1932	1933
−2.0	4.840	5.707	5.869	5.655	5.737	4.641	4.932	4.914	5.333	5.524
−1.0	3.222	3.635	3.651	3.496	3.582	3.061	3.113	3.003	3.513	3.406
0	1.340	1.410	1.220	1.197	1.336	1.076	1.010	0.839	1.300	1.095
0.2	0.927	0.935	0.700	0.704	0.860	0.645	0.570	0.387	0.821	0.611
0.4	0.504	0.449	0.168	0.198	0.376	0.202	0.125	−0.071	0.328	0.119
0.6	0.069	−0.048	−0.373	−0.321	−0.119	−0.250	−0.326	−0.536	−0.178	−0.381
0.8	−0.376	−0.557	−0.924	−0.855	−0.623	−0.712	−0.783	−1.007	−0.698	−0.890
1.0	−0.833	−1.077	−1.483	−1.404	−1.138	−1.186	−1.246	−1.486	−1.234	−1.408
1.6	−2.274	−2.710	−3.209	−3.145	−2.729	−2.655	−2.672	−2.968	−2.941	−3.010
2.0	−3.293	−3.858	−4.396	−4.390	−3.845	−3.682	−3.660	−3.997	−4.174	−4.116

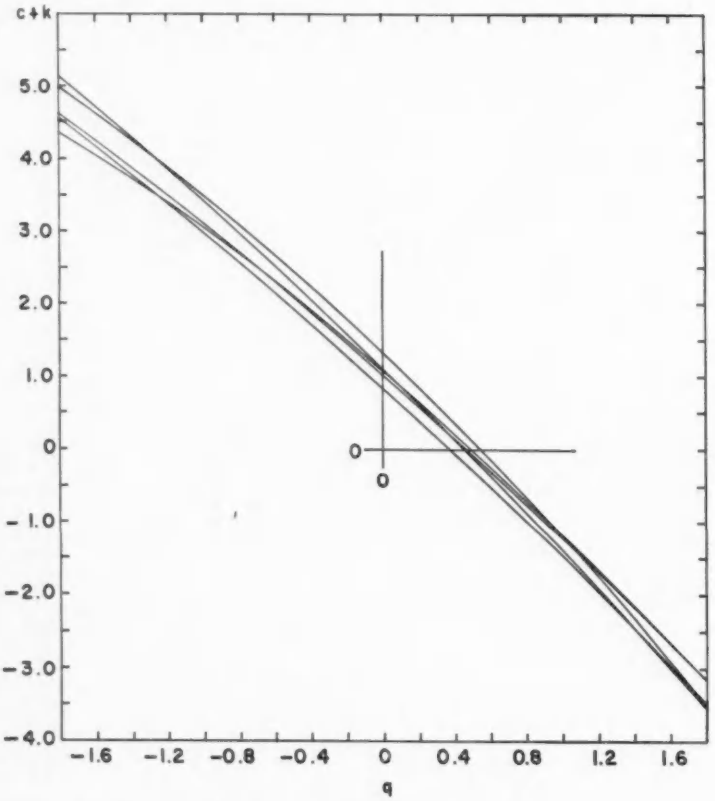

FIG. 4. Loci of $c + k = f(q)$, Karluk 3-annuli sockeye smolts.

TABLE IV. Maximum values of q, $c + k$. Karluk sockeye. Values of max. (q) are from graphical interpolation.

Smolt year	2-annulus smolts		3-annulus smolts	
	max. (q) ($c + k = 0$)	max. ($c + k$) ($q = 0$)	max. (q) ($c + k = 0$)	max. ($c + k$) ($q = 0$)
1929	0.631	1.340	0.490	1.076
1930	0.581	1.410	0.454	1.010
1931	0.461	1.220	0.368	0.839
1932	0.476	1.197	0.530	1.300
1933	0.552	1.336	0.447	1.095

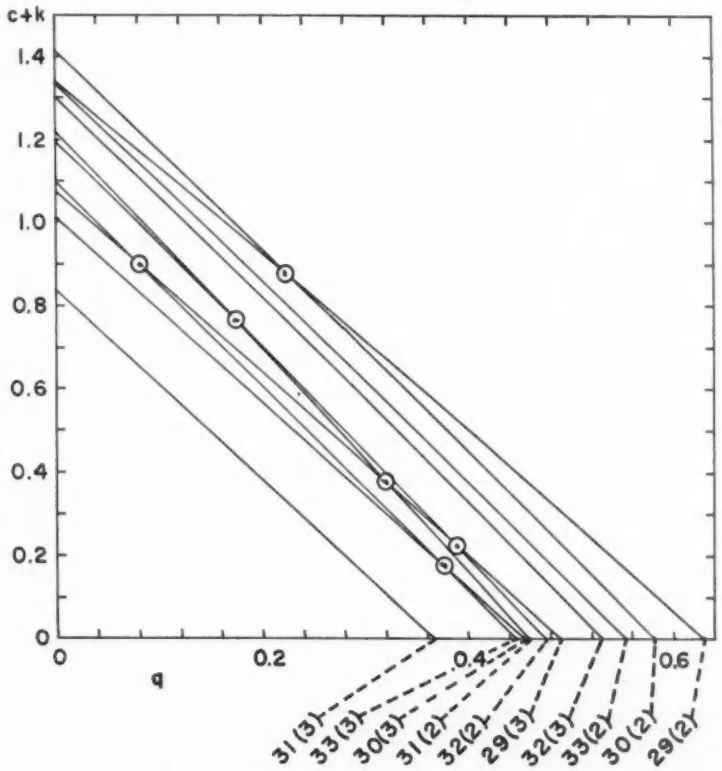

FIG. 5. Loci of $c + k = f(q)$ for Karluk sockeye.

Enlarged portions of the curves shown in Fig. 3 and 4 are presented in Fig. 5. Maximum values of q and $c+k$ are presented in Table IV. Intersections between lines are indicated by a point enclosed within a circle in Fig. 5. These values, as determined by linear interpolation, are presented in Table V. Some

slight priorities might be assigned among these solutions under a variety of hypotheses re time at sea, size of smolts, etc. But when it is considered that *all* data, including the number of smolts marked of any particular group, are subject to sampling error, it appears unprofitable to place any preference on these values. Rather, the average of values of q and $c+k$ are presented in the last line of Table V as the best available estimate of mortality rates affecting the Karluk sockeye in the marine environment.

TABLE V. Solutions of q, $c + k$ resulting from paired equations. Karluk sockeye. Values are from graphic interpolation of intersects.

Pair	q	$c + k$
1929(2), 1930(2)	0.223	0.879
1931(2), 1932(2)	0.176	0.761
1929(3), 1933(3)	0.082	0.900
1930(3), 1933(3)	0.378	0.173
1929(3), 1931(2)	0.325	0.368
1929(3), 1932(2)	0.390	0.224
Average	0.262	0.551

DALNEE SOCKEYE

Krogius and Krokhin (1948) reported numerical estimates of smolts migrating from the Dalnee River, Kamchatka. These estimates resulted from trap nets in the river; age assignment was done on the basis of ratios derived from samples. Returning adults taken in the fisheries of the Dalnee River and counted at a weir formed the basis of estimated numbers returning from a given smolt group. These data are summarized in Table VI. In the general description of the Dalnee sockeye, Mrs Krogius gave the period of maximum migration of 1-annulus smolts as July 10–15 and of 2-annuli smolts as June 20–30. A "very small" portion of the adults return in May and early June. The main returning adult run occurs in the period mid-July to mid-August. For the present purposes the length of the final year, as measured from the average date of smolt migration, is taken as 0.04 years for the 1-annulus group and as 0.10 for the 2-annuli group of smolts.

Data presented on Dalnee sockeye are incomplete in that only numerical estimates of the main groups (1/2, 1/3, 2/2, 2/3) were given. Mention was made of the 2/1 group as being insignificant and variable. Columns in Tables 14 and 18 of Krogius and Krohkin contain estimates labelled "other" age groups but it is not possible to make any assignment to a given smolt migration. Furthermore, Dr Krogius states, "Prior to 1943 the size of the industry varied relatively slightly; in 1943 it experienced a radical change; the Japanese catch in the sea along the coast of Kamchatka was cut off, which sharply increased the coefficient of return". Also, while the estimated returns include catches by fisheries in the

Dalnee River, catches of Dalnee sockeye made in the Paratunka River, Avachi Gulf, or "outside", were not included. These were described as "in general quite a considerable quantity". Thus in estimating mortality rates for the Dalnee sockeye, the grilse and the unknown effects of the fisheries are included in the estimates of natural mortality.

TABLE VI. Dalnee sockeye data. Data from Krogius and Krokhin (1948), tables 14 and 18.

Year of smolt migration (t_0)	Calculated number of smolts (N_0)	Calculated returns after	
		2 years (R_2)	3 years (R_3)
	Smolts with 1 freshwater annulus		
1936	85,000	14,000	14,500
1937	128,000	16,700	20,300
1938	113,000	33,300	11,100
1939	23,000	2,400	3,800
1940	68,000	14,900	17,600
	Smolts with 2 freshwater annuli		
1936	200,000	41,600	10,100
1937	86,000	28,300	4,000
1938	169,000	29,200	6,200
1939	131,000	38,300	4,500
1940	34,000	9,500	3,300

TABLE VII. Values of $c + k = f(q)$. Dalnee sockeye.

	1-annulus smolts					2-annuli smolts				
q	1936	1937	1938	1939	1940	1936	1937	1938	1939	1940
−2.0	5.769	5.980	5.275	6.162	5.466	5.735	5.290	5.924	5.412	5.424
−1.0	3.521	3.707	3.146	3.841	3.215	3.585	3.161	3.780	3.287	3.255
0	1.093	1.241	0.934	1.311	0.738	1.353	0.979	1.563	1.119	0.977
0.2	0.578	0.718	0.472	0.776	0.217	0.891	0.532	1.105	0.676	0.501
0.4	0.053	0.186	0.002	0.231	−0.314	0.421	0.080	0.641	0.228	0.018
0.6	−0.481	−0.355	−0.477	−0.321	−0.854	−0.056	−0.378	0.169	−0.224	−0.475
0.8	−1.024	−0.882	−0.965	−0.881	−1.403	−0.542	−0.842	−0.311	−0.683	−0.978
1.0	−1.575	−1.463	−1.463	−1.448	−1.960	−1.037	−1.314	−0.800	−1.147	−1.490
1.6	−3.272	−3.176	−3.017	−3.184	−3.670	−2.579	−2.779	−2.323	−2.589	−3.086
2.0	−4.434	−4.344	−4.100	−4.362	−4.837	−3.657	−3.804	−3.388	−3.595	−4.197

Data of Table VI, together with the estimates of t, form the basis of calculations of $c+k = f(q)$ presented in Table VII. Loci of the functions are shown graphically in Fig. 6 for the area between the limits [q, $c+k = 0$]. As shown by Fig. 6, the computed mortality rates are quite variable, more so than those of the Karluk sockeye (Fig. 5). Limit values are given in Table VIII. Solutions of paired equations within the limit area are presented in Table IX, together with their average.

TABLE VIII. Maximum and minimum values of q, $c + k$. Dalnee sockeye. Values of max. (q) are from graphic interpolation.

Smolt year	1-annulus smolts		2-annulus smolts	
	max. (q) ($c + k = 0$)	max. ($c + k$) ($q = 0$)	max. (q) ($c + k = 0$)	max. ($c + k$) ($q = 0$)
1936	0.421	1.093	0.577	1.353
1937	0.469	1.241	0.435	0.979
1938	0.402	0.934	0.670	1.563
1939	0.484	1.311	0.501	1.119
1940	0.282	0.738	0.407	0.977

TABLE IX. Paired solutions of $c + k$, q. Dalnee sockeye. Values are from graphic interpolation of intersects.

Pair	q	$c + k$
1936(1), 1937(2)	0.318	0.268
1937(1), 1939(2)	0.298	0.455
1939(1), 1939(2)	0.417	0.190
Average	0.344	0.304

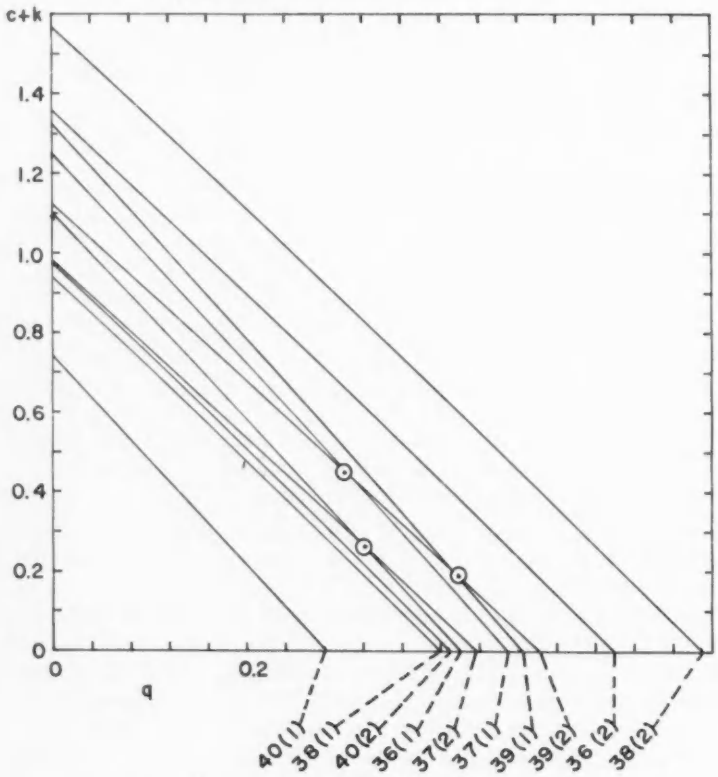

FIG. 6. Loci of $c + k = f(q)$ for Dalnee sockeye.

CULTUS LAKE SOCKEYE

Foerster (1936a) reported the returns from two marking experiments on Cultus Lake sockeye smolts. Classification by freshwater age is not available; thus no division into subgroups is possible. Data were presented allowing classification by sex; however, this treatment led to an estimate of q, $c+k$ lying outside the limit area. As remarked by Foerster (1936a, p. 36), a differential mortality appeared to exist which favoured the survival of females and could not be explained on the basis of selective fishing or the early maturation of grilse. Because of these difficulties the experiments were left classified only by year of smolt migration. These statistics are presented in Table X.

TABLE X. Cultus Lake sockeye. Data from table I of Foerster (1936a).

Year of smolt migration (t_0)	Number of smolts marked (N_0)	Reported returns after		
		1 yr (R_1)	2 yr (R_2)	3 yr (R_3)
1930	104,061	28	3,749	44
1931	365,265	41	12,017	674

In obtaining the estimates of catch, Foerster sampled for marks at several locations along the routes of migrating salmon, examining in some cases a large portion of the catch. Escapements were based on individual examination of the adults as they entered Cultus Lake which were either released or artificially spawned for hatchery egg supply. The main possible sources of error appear to be from an unknown but small personal use catch of the adults below Cultus Lake, straying or non-homing, and sampling of the commercial catches. These errors, if they existed, were believed to be small.

Foerster (1936a) gives the time of 50% seaward migration in 1930 as April 26, and in 1931 as April 12. The approximate dates of 50% recovery of marks in the Fraser River fishery may be taken as estimates of the end of the period spent at sea. This has been estimated from Tables II and III of Foerster (1936a) as September 20 in both 1932 and 1933, the years covering the largest portion of the returning adults. The average time spent in the sea during the final year was, for the 1930 group, 0.41 year and for the 1931 group, 0.44 year. A correction coefficient of 1.27 was used to adjust for marking. From the data presented in Table X and the adjustments for t and marking, values of $(c+k) = f(q)$ were computed and are presented in Table XI. The loci of $c+k = f(q)$ are graphically presented in Fig. 7. In the case of Cultus sockeye the lines are very nearly parallel indicating only slight differences in maturity schedule between groups. However, they do intersect at $q \simeq 0.466$, $c + k \simeq 1.474$. The limits of q and $c + k$, together with the above best estimate, are given in Table XII. While the graphic solution of q, $c + k$ from the paired equations lies within the limit area, the two groups were so similar that a slight difference in mortality rates would seriously alter the point of intersection.

TABLE XI. Values of $c + k = f(q)$, adjusted for marking effect. Cultus sockeye.

q	1930	1931
−2.0	7.365	7.532
−1.0	5.004	5.107
0	2.602	2.643
0.2	2.119	2.144
0.4	1.634	1.641
0.6	1.149	1.134
0.8	0.662	0.622
1.0	0.173	0.104
1.6	−1.307	−1.496
2.0	−2.313	−2.615

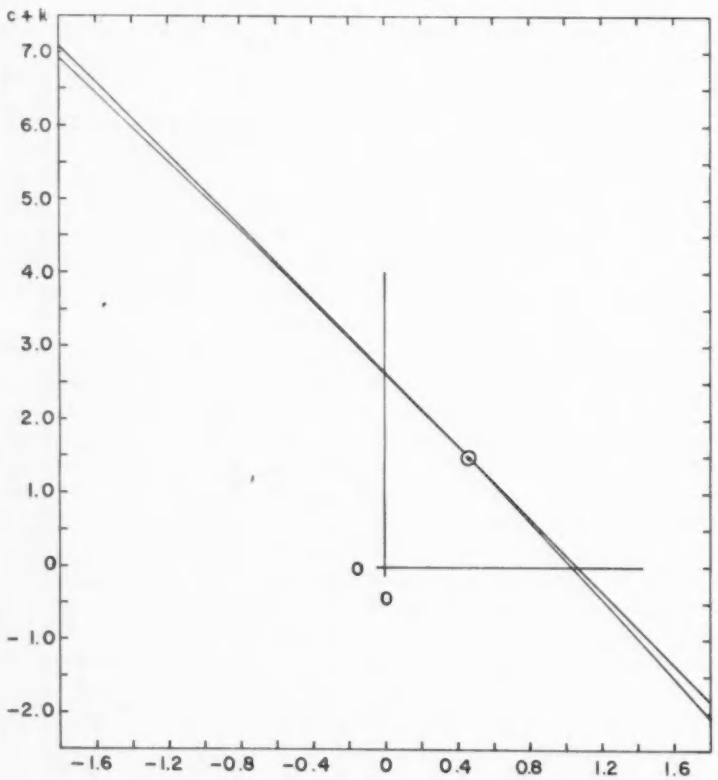

FIG. 7. Loci of $c + k = f(q)$ for Cultus sockeye.

TABLE XII. Maximum and minimum values of q, $c + k$. Cultus sockeye. Values of max. (q) are from graphic interpolation.

Smolt year	max. (q) ($c + k = 0$)	max. ($c + k$) ($q = 0$)
1930	1.070	2.602
1931	1.039	2.643
Intersect	$q = 0.466$	$c + k = 1.474$

CHILKO SOCKEYE

Henry (1961) has estimated the returns from several brood years of the Chilko race of Fraser River sockeye on the basis of identifying scale characteristics. Data for 1-annulus smolts (from Henry's tables 20 and 26) have been corrected (from data presented in Henry's table 15) to estimate total returns from the brood years 1950 to 1954 and are presented in Table XIII. Time of 50% adult returns is estimated as approximately August 1 (from fig. 19, Henry, 1961 and fig. 15, Killick, 1955). The approximate 50% date of smolt migration is estimated at May 1 (figs. 37, 38, Clutter and Whitesel, 1956). Average time in the sea during the final year is, then, approximately 0.25 year. From these data values of $c + k = f(q)$ are computed using Eqn. (13) and are presented in Table XIV.

TABLE XIII. Chilko sockeye. Data from Henry (1961), 1 freshwater annulus smolts.

Year of smolt migration t_0	Estimated smolts N_0	Estimated returns after		
		1 yr R_1	2 yr R_2	3 yr R_3
1952	1,170,490	1,078	180,005	4,644
1953	11,581,930	2,676	644,666	20,567
1954	24,688,406	20,032	1,775,467	31,911
1955	8,316,130	1,150	511,062	11,221
1956	2,997,249	3,923	503,287	4,612

TABLE XIV. Values of $c + k = f(q)$, Chilko sockeye.

q	Smolt year					Average
	1952	1953	1954	1955	1956	
−2.0	6.326	7.355	7.050	7.271	6.228	6.846
−1.0	4.097	5.116	4.846	5.025	4.010	4.619
0	1.841	2.853	2.376	2.766	1.767	2.321
0.2	1.387	2.397	2.152	2.312	1.317	1.913
0.4	0.931	1.939	1.699	1.856	0.865	1.458
0.6	0.473	1.480	1.244	1.399	0.413	1.002
0.8	0.014	1.018	0.788	0.941	−0.059	0.540
1.0	−0.448	0.554	0.331	0.481	−0.493	0.085
1.6	−1.849	−0.859	−1.055	−0.914	−1.862	−1.308
2.0	−2.803	−1.824	−1.994	−1.862	−2.782	−2.253

Examination of Table XIV discloses no intersections of loci. Mortality rates were variable. Variation cannot be assigned to either $c + k$ or q. Average values of $c + k = f(q)$ are given in the last column of Table XIV.

HOOKNOSE CREEK SOCKEYE

In 1949 and 1955 all sockeye smolts passing a weir at the mouth of Hooknose Creek, British Columbia, were marked by the removal of a combination of adipose and ventral fins. In subsequent years adult sockeye surviving from these smolt groups were enumerated and sexed as they re-entered the stream. No data are available for separating the populations on the basis of smolt age; however, if a smolt sex ratio of 1:1 is assumed[4], the smolt populations and their returning adults can be subdivided into groups containing like sex. No search was made in the fishery for these marks; however, from estimates of catches and escapements of sockeye in the general area, as reported by the Canada Department of Fisheries, the general level of fishing mortality on this species has been estimated. Counted escapements and estimated returns from these experiments are summarized in Table XV.

TABLE XV. Estimated returns of marked Hooknose sockeye smolts. Data given as E_t are weir counts of returning adults. The ratio E/R is developed from Canadian Department of Fisheries estimates of Area 8 catch and escapement. For those fish returning as grilse the alternative hypotheses of (a) 100% escapement, and (b) no selectivity of the fishery, have been followed as limits of the true ratio for these small fish.

Smolt migration t_0	Estimated no. of smolts marked N_0	Year of return								
		1			2			3		
		E_1	E_1/R_1	R_1	E_2	E_2/R_2	R_2	E_3	E_3/R_3	R_3
1949 ♂	9743	194	(a) 1	194	174	0.44	395	3	0.35	9
			(b) 0.44	441						
1949 ♀	9743	0	...	...	214	0.44	486	30	0.35	86
1955 ♂	6890	151	(a) 1	151	248	0.77	322	0	...	...
			(b) 0.46	328						
1955 ♀	6890	0	...	...	314	0.77	408	2	0.10	20

Difficulty is encountered in adjusting the escapements of grilse to an estimate of return. In the Hooknose Creek area, fishing was primarily with purse seines which, on the older adults, may be considered non-selective as to size. Many of the grilse returning to the stream, however, were net-marked, clearly indicating a previous encounter with the seines. Two assumptions may be followed: (a) that fishing mortality on the grilse was nil; (b) that fishing mortality on the grilse

[4]This assumption is probably valid. At Hooknose Creek in 1949 J. G. Robertson (unpublished data) found that 51.69% of a sample of 277 sockeye smolts were males, not a significant departure from equality.

was equal to that on the larger adults. Grilse may be observed in the catches but not in the same proportions to large adults as in the escapements. Further, experiments with related species have demonstrated the occurrence of death resulting from fatigue (Parker and Black, 1959; Parker *et al.*, 1959) and the net-marked grilse in the escapement are probably but a fraction of those encountering and escaping the nets. From these arguments, the above assumptions are thought to serve as limits of the most likely situation, i.e., fishing mortality on grilse is less than that for the large adults but greater than zero. These limits are followed through Table XV and in subsequent calculations.

The coefficient for marking (1.27) discussed earlier as resulting from Cultus sockeye experiments has been borrowed to correct for the effect of marking on the Hooknose sockeye smolts. Values of $c+k = f(q)$ are presented in Table XVI where the subscripts (a) and (b) are used to denote the results from the two assumptions[5] re fishing mortality.

TABLE XVI. Values of $c + k = f(q)$, adjusted for marking. Hooknose sockeye.

q	1949			1955		
	♂a	♂b	♀	♂a	♂b	♀
−2.0	5.446	4.833	6.850	5.386	4.839	6.723
−1.0	3.975	3.509	4.573	3.889	3.456	4.465
0	2.197	1.925	2.232	2.109	1.859	2.188
0.2	1.803	1.571	1.748	1.718	1.504	1.727
0.4	1.397	1.202	1.257	1.316	1.136	1.264
0.6	0.981	0.819	0.758	0.906	0.756	0.797
0.8	0.554	0.422	0.247	0.489	0.365	0.326
1.0	0.118	0.012	−0.274	0.065	−0.036	−0.151
1.6	−1.244	−1.294	−1.912	−1.235	−1.287	−1.625
2.0	−2.199	−2.228	−3.066	−2.117	−2.149	−2.655

In Table XVII are presented maximum and minimum limits of $[q, c + k]$. The loci of $c + k = f(q)$ are plotted in Fig. 8. From a consideration of Fig. 8 it may be stated that mortalities affecting the 1949 and 1955 smolt populations were quite similar. While the locus of $c + k = f(q)$ for the 1949 males lies entirely below that of the 1955 males, the lines depicting the relationship for females intersect at approximately (3.351, 1.379). These results are not surprising when the adjustments and assumptions involved are considered; it might be caused simply by a departure from 1:1 sex ratio in the smolts.

The lines are close enough to provide 8 intersections out of a possible 9 within the limited zone[6]. The 1949 ♂$_a$ × 1955 ♀ pairing leads to a negative value

[5]The subscript (a) denotes the upper limit resulting from the assumption of no fishing mortality on grilse; (b) denotes the lower limit which results from the assumption of equal fishing mortality on all segments of the stock within any single year.

[6]Since by different assumptions re fishing mortality on grilse the combinations of pairs involving both ♂$_a$ and ♂$_b$ cannot be considered as possibilities.

of $q = -0.026$. In calculating the average values of q, $c+k$ to depict a best generalized estimate, the use of $\sigma^{\prime}_{a}$ must be accompanied by the use of $\sigma^{\prime}_{b}$–for in this case, the data being approximately linear within the limits, the average of the two assumptions is used. Accordingly, as the solution resulting from 1949 $\sigma^{\prime}_{a}$ and 1955 ♀ yields a negative value for q, the pair 1949 $\sigma^{\prime}_{b}$ and 1955 ♀ must be discarded from further consideration. The remaining pairs and their averages are presented in Table XVIII. In averaging the values of $c + k = f(q)$, a weighting factor of 2 has been used on the statistics for females together with the estimates of $c + k = f(q)$ for assumptions (a) and (b).

TABLE XVII. Maximum and minimum values of q, $c + k$. Hooknose sockeye. Values of max. (q) are obtained by linear interpolation.

Smolt group	Sex	max. (q) ($c + k = 0$)	max. ($c + k$) ($q = 0$)
1949	$\sigma^{\prime}_{a}$	1.053	2.197
	$\sigma^{\prime}_{b}$	1.006	1.925
	♀	0.895	2.232
1955	$\sigma^{\prime}_{a}$	1.030	2.109
	$\sigma^{\prime}_{b}$	0.982	1.859
	♀	0.937	2.188

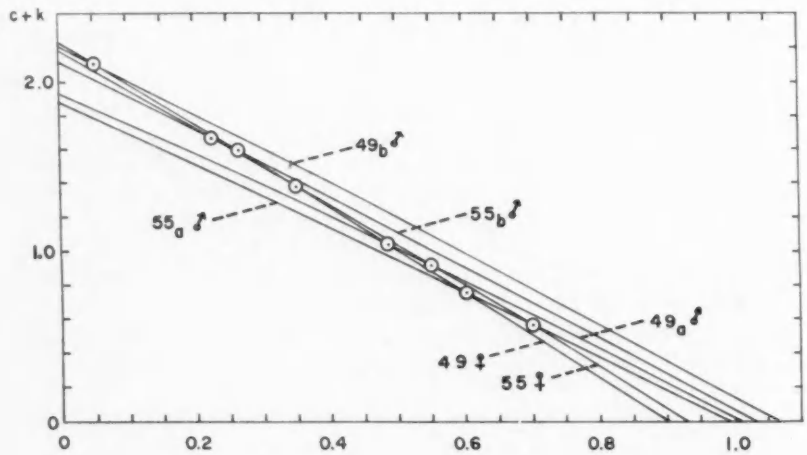

FIG. 8. Loci of $c + k = f(q)$ for Hooknose sockeye.

TABLE XVIII. Solutions of q, $c + k$ from paired equations, by graphic interpolation. Hooknose sockeye.

Pair	q	$c + k$
1949 ♂a, 1949 ♀	0.078	2.044
1949 ♂b, 1949 ♀	0.495	1.020
1955 ♂a, 1955 ♀	0.267	1.584
1955 ♂b, 1955 ♀	0.704	0.552
1955 ♂a, 1949 ♀	0.230	1.658
1955 ♂b, 1949 ♀	0.605	0.746
1949 ♀ , 1955 ♀	0.351	1.379
Average	0.390	1.283

BARE LAKE SOCKEYE

Nelson (1959) has presented smolt counts and calculated returning adult populations for sockeye salmon of Bare Lake, Kodiak Island, Alaska. These data apply to the migrants as they departed and entered the lake, and include mortality occuring over about 10 miles of the very small and shallow Bare Creek, about the same distance over the much larger Red River in addition to marine mortality. Both smolt and adult migrations occurred mainly in June, hence periods of whole years are applicable to the model. Data for smolt runs and adult returns, based on data contained in Nelson's Tables 4 and 8, are presented in Table XIX. From these data values of $c + k = f(q)$ are computed using equation (13) and are presented in Table XX for individual smolt populations and their average. There are no intersections of loci to indicate specific values of q or $c + k$.

TABLE XIX. Bare Lake sockeye. Data from Nelson (1959).

Year of smolt migration	Number of smolts	Estimated returns 2 yr	3 yr	4 yr
t_0	N_0	R_2	R_3	R_4
1950	10,199	43	290	0
1951	4,503	45	160	0
1952	8,620	116	340	1
1953	5,058	99	300	0

TABLE XX. Values of $c = k\ ½\ f(q)$, Bare Lake sockeye.

q	1950	1951	1952	1953	Average
0	3.422	3.090	2.937	2.540	2.997
.2	2.845	2.530	2.384	1.986	2.436
.4	2.265	1.965	1.823	1.425	1.870
.6	1.682	1.348	1.257	0.859	1.286
.8	1.096	0.818	0.685	0.287	0.722
1.0	0.507	0.239	0.108	−0.290	0.141
1.2	−0.084	−0.344	−0.474	−0.870	−0.443

HOOKNOSE CREEK PINKS AND CHUMS

Hunter (1959) has presented the results of marking pink and chum fry (1948 brood year) in the spring of 1949. These are presented in Table XXI. A marking coefficient of 1.52 was computed from the relation of returns from marked and unmarked pinks (Parker *et al.*, 1962) and has been also applied to the marked chum group. The time period for the ultimate year is approximately 0.4 year for both species. Values of $c + k = f(q)$ for these two sets of data are presented in Table XXII. Graphs of the functions are presented in Fig. 9. Values of the limits of $[c + k, q]$ are given in Table XXII.

TABLE XXI. Estimated returns of marked Hooknose pink and chum fry from data of Hunter (1959). The fraction E_t/R_t is assumed to be 0.35. 1948 brood year.

Species	Number marked N_0	Year of return							
		1950		1951		1952		1953	
		E_1	R_1	E_2	R_2	E_3	R_3	E_4	R_4
Pink	10,787	103	294						
Chum	54,831	0	0	51	146	186	531	22	63

TABLE XXII. Values of $c + k = f(q)$, adjusted for marking. Hooknose pinks and chums, 1948 brood year.

q	Pinks	Chums
−2.0	5.095	8.484
−1.0	3.695	5.824
0	2.295	2.742
0.2	2.015	2.076
0.4	1.735	1.394
0.6	1.455	0.694
0.8	1.175	0.022
1.0	0.895	−0.776
1.6	0.055	−3.066
2.0	−0.505	−4.689

If pink and chum salmon are subject to similar mortality rates at sea, which appears at least superficially tenable (Parker, 1962), then these data may be used to obtain a direct solution of q, $c + k$ which satisfies both equations. This point is indicated by the intersection of the lines in Fig. 9 at the values $q = 0.231$, $c + k = 1.970$. These data are subject to the accustomed errors inherent in the previous estimates; thus no degree of confidence is placed on this estimate alone.

Using the arguments (Neave, 1953) that (1) fecundity of a species results from natural selection and reflects the average hazards to survival, (2) the ecological similarity of pink and chum salmon and (3) the 15 years of observations

of freshwater survival for these species at Hooknose Creek, Parker (1962) presented an estimated schedule of mortality rates to hold the populations at equilibrium levels. From these estimates the values of $q = 0.201$ and $c + k = 2.86$ are derived. This point is indicated in Fig. 9 as a dot enclosed by a circle.

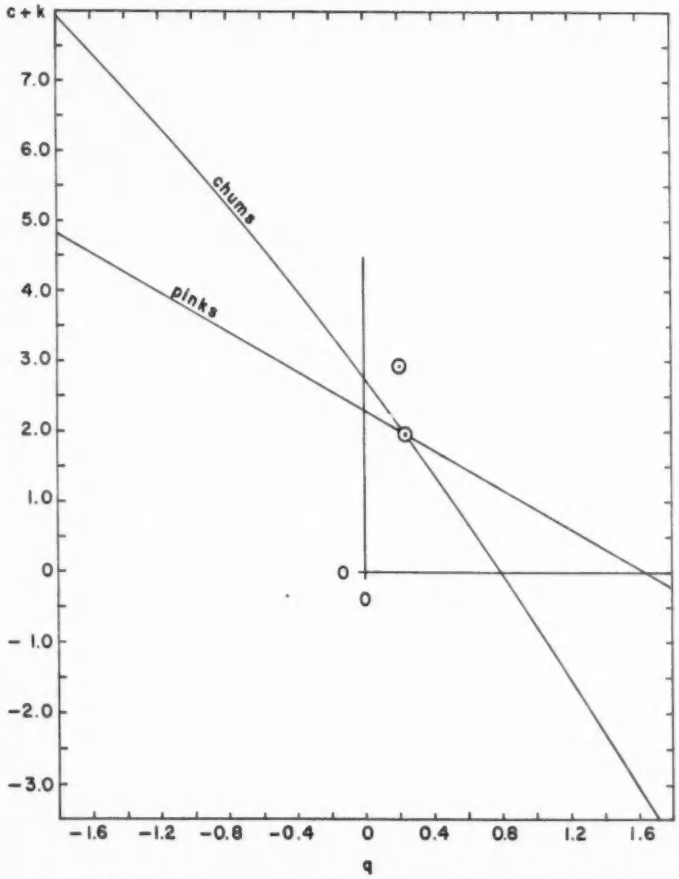

FIG. 9. Loci of $c + k = f(q)$ for Hooknose pink and chum salmon.

NORTHERN CHINOOK SALMON

Parker and Kirkness (1956) and Parker (1960) estimated the annual survival rate of *tagged* chinook salmon at S = 0.659, corresponding to an instantaneous mortality rate of 0.417. While the treatment eliminated the immediate effects of marking, the long-term effects are unknown and inherent in the estimate. The estimate applies directly to the factors $q + k$, i.e., describes mortality from natural causes exclusive of fishing. In the case of chinook much of the sea

period is spent in close proximity to the coast or within "inside" waters. In this situation the coastal factor c becomes k during the period at sea. Since c has been described as applying to young fish of smolt or slightly larger size, by the time chinook are taken on commercial gear the coastal factor is called k. According to previous treatment the limits of $[q, k]$ are 0 and 0.417 and for each assumed value of q within the limits k takes a definite value, i.e., $k = f(q)$ and the function is $k = 0.417 - q$.

CALIFORNIA COHO SALMON

Murphy (1952) presented a series of counts of adult coho salmon, extending from 1938 to 1951, taken at Benbow Dam, California. These counts were of numbers of male, female and grilse ascending the fishway. By assuming similar mortality rates re sexes and that prior to the grilse migration the sex ratio of survivors of any smolt population was 1:1, Murphy reasoned that the difference in numbers of older males and females should be equal to the previous year's grilse count multiplied by the survival coefficient (S) for the final 12-month period in the sea. Thus Murphy's equation,

$$S = \frac{♀_n - ♂_n}{♂_n - 1}$$

was used to compute S for 12 years of suitable records. Estimates varied from 0.158 to 0.569 with a geometric mean of 0.330. These estimates include fishing as well as natural sources of mortality. As with the chinook, at least a large portion of coho reside near the coast during sea life; thus in instantaneous rates, $q + k + p = 1.108$. In addition to the assumptions Murphy listed three possible sources of error: (a) misclassification of sex, (b) mortality of grilse during the spawning migration, and (c) straying. Only the first was thought to be of possible significance.

Murphy's treatment is related to the solution of simultaneous equations (equations 14a, 14b) and was, in fact, one basis for development of the present treatment of salmon mortality. While the coho mortality estimates, because they contain the unknown factor of fishing mortality (p), are not directly comparable to the estimates developed for the other salmon species, they are compatible with the chinook estimate as may be seen by letting the rates $q + k$ be equal for the two species leaving $p = 0.691$ or equivalent to an annual fishing mortality rate of 49.9%. While this is not an accurate figure neither is it unreasonable. Because of this uncertainty, however, the coho mortality estimates are not useful in the present comparison except to note their compatibility with that for chinook.

INTER- AND INTRA-SPECIES COMPARISON

Lines depicting the average relationship, $c + k = f(q)$, for each of the stocks previously discussed are presented in Fig. 10. Estimates of q and $c + k$ resulting from the average of solutions of paired equations for each stock are presented as dots enclosed by a circle. The estimate of q and $c + k$ for pinks and chums based on fecundity comparisons is also included as a dot enclosed by a circle. All of

these estimates are subject to the same type of errors in sampling and inherent assumptions; yet only one set of values—that for Cultus sockeye—lies outside a range of q common to all the populations considered. A glance at Fig. 7 demonstrates the similarity between these two groups of salmon in respect to maturity schedules. A very slight difference in either q, or $c + k$, would shift the point of intersection considerably.

On the other hand, relatively great differences appear to characterize the estimates of $c + k$. This is principally exemplified in a comparison between British Columbia stocks and those of Karluk and Dalnee Rivers. It is therefore suggested that ocean mortality may be relatively constant and similar for Pacific salmon while the coastal factor, $c + k$, is markedly different between species and geographic locations.

TABLE XXIII. Maximum and minimum values of q, $c + k$ for Hooknose pink and chum salmon. Values of max. (q) are estimated by graphical interpolation.

Group	max. (q) ($c + k = 0$)	max. ($c + k$) ($q = 0$)
Pink salmon	1.639	2.295
Chum salmon	0.806	2.742

For an average figure, to characterize ocean mortality of salmon, values of q indicated in Fig. 10 were averaged without weighting. The result is indicated by a dashed ordinate at $q = 0.316$. If this average value of q can be accepted as the best available estimate then k, as depicted by chinook, is quite small—approximately 0.1 on an annual basis. As the other populations are within the coastal area as adults for a period of time approximating 2 months, the value of k for sockeye, chum and pink salmon can be estimated as approximately 0.017. Using the average values of $q = 0.316$ and $k = 0.017$, values of c for each population have been estimated by graphic interpolation and are presented as Table XXIV.

TABLE XXIV. Values of coastal mortality, c, for sockeye, chum and pink salmon, estimated from linear interpolation at $q = 0.316$, $k = 0.017$

Population	c
Dalnee sockeye	0.34
Karluk sockeye	0.42
Hooknose sockeye	1.43
Chilko sockeye	1.64
Cultus sockeye	1.83
Bare Lake	2.10
Hooknose chums	1.67
Hooknose pinks	1.83

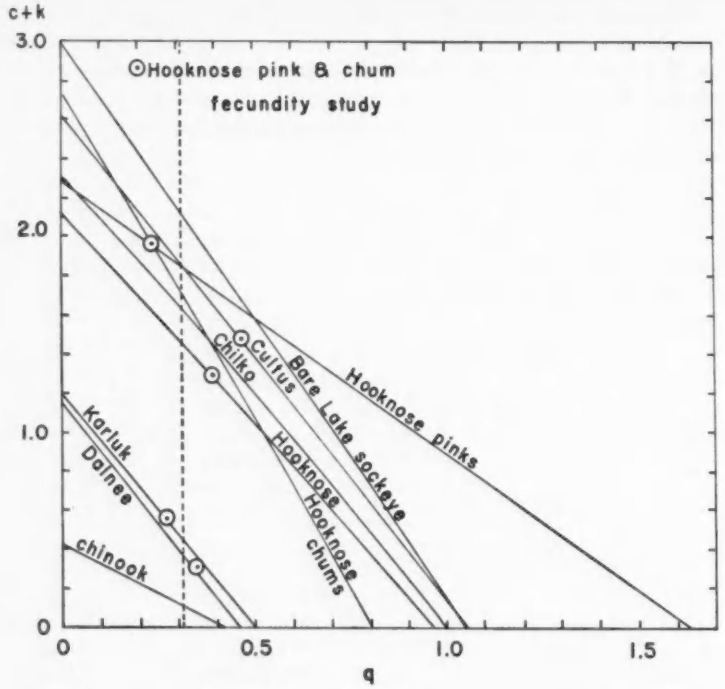

FIG. 10. Averages of loci of $c + k = f(q)$ for Pacific salmon. For chinook $k = f(q)$.

DISCUSSION

The series presented in Table XXIV are not without interest, for the estimated magnitude of c, at least for the North American stocks, reflects the type of coastal geography encountered by the population it depicts. Karluk sockeye, which enter the open sea immediately after leaving fresh water, are characterized by a relatively low value of c. On the other extreme, Cultus and Chilko sockeye enter the Strait of Georgia, an enclosed sea, and must travel more than 100 miles by most direct route to leave the coastal waters. Hooknose sockeye are intermediate in both c value and geographical situation. The values of c for pinks and chums result from a single year's marking and, judging from survival data presented by Hunter (1959, table XXII), the 1948 brood year was subjected to less-than-average sea mortality. For pinks and chums the position of q, $c + k$ based on the fecundity comparison may better represent their average mortality conditions. It is possible, then, that the series also reflects differences due to size, although differences in time spent in the coastal area may provide the underlying mechanism. While at first the Bare Lake sockeye appear to provide an exception to this generalization, it must also be considered that, in this case, the value c includes migration through a very shallow and exposed stream.

In what has preceded a number of mortality estimates have been made using data subject to severe sampling errors and omissions. The validity of these estimates also rests on several assumptions about which nothing can be definitely stated. These data, however, represent many years of effort and collectively may be considered as extensive. As a result of this study it is doubted that mortality rates can be more accurately defined by any repetition of the experiments and observations outlined. A more direct approach designed to measure mortality directly during short intervals of time is needed, and such experiments must be repeated often enough to describe annual variability.

CONCLUSIONS

At the present time it appears valid to generalize by the following statements to pertain to Pacific salmon.

1. Ocean mortality is relatively constant and is of the order of magnitude $q = 0.32$, S = 73% annually.
2. A coastal mortality factor, c, applying to the small juveniles, apparently exists and is characteristic of the species and race through the media of size, time spent in the coastal area, and geography.
3. A coastal factor, k, applying to the large salmon, may exist but is of negligible influence on the total mortality rate.

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Proteins in Fish Muscle
17. Fractionation of Aqueous Extracts with Zinc Acetate [1,2]

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ABSTRACT

Zinc acetate in low concentrations has been used to fractionate aqueous extracts of cod and haddock muscle. Approximately 18% of the cod proteins extracted remained soluble after addition of 0.1*M* zinc acetate and subsequent treatment with KH_2PO_4 buffer. This fraction consisted largely of two components of the original cod extract, and the same fraction from haddock was very similar. Fractionation on DEAE-cellulose removed the minor components, but failed to separate the main ones. The protein of the cod fraction contained an unusually large proportion of phenylalanine.

Relatively little progress has been reported so far in separating and identifying the various components of aqueous extracts of fish muscles, which are presumably derived from the sarcoplasm of the muscle. Jebsen and Hamoir (1958) have investigated the electrophoretic and ultracentrifugal behaviour of such an extract of plaice (*Pleuronectes platessa* L.) muscle, and of fractions prepared from it with neutral ammonium sulphate over the whole range of saturation. Nikkilä and Linko (1955) have used paper electrophoresis to follow fractionation of pike (*Esox lucius*) muscle albumins by ethanol at low temperatures, and apparently succeeded in separating the principal components on a small scale. A protein of low molecular weight and peculiar amino acid composition has been isolated from aqueous extracts of muscle of carp (*Cyprinus carpio*) and of plaice (Henrotte, 1955; Hamoir, 1957; Jebsen and Hamoir, 1958). Henrotte (1952, 1954) succeeded in crystallizing from an extract of carp albumins a component that had an electrophoretic mobility corresponding to the main peak in the water-dialyzed extract. Crystals of the pigmented protein, myoglobin, have been prepared from the red muscle of carp (Hamoir, 1955a, b), and Huys (1954) achieved the complete purification of a similar protein from tuna (*Thunnus thynnus*).

Cohn *et al.* (1950, 1953) introduced the use of heavy metals as a means of fractionating the proteins of biological fluids, especially human blood, but this procedure appears to have been used rather sparingly since then. As part of a general study of the water extracts of fish muscle, we have investigated the use of zinc acetate as a means of fractionating their dissolved components.

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[2]Papers Nos. 1 to 15 of this series appeared in This Journal, paper No. 15 being in Vol. 16(2): 243–246, 1959. Paper No. 16 appeared in *Canadian J. Biochem. Physiol.*, Vol. 38: 1437–1447, 1960.

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MATERIALS AND METHODS

Fish

Fillets were cut from cod (*Gadus callarias*) and haddock (*Melanogrammus aeglefinus*) of small to medium size (12 to 24 in; 30 to 61 cm). The haddock and some of the cod were commercial samples and in post-rigor condition; the remaining cod were freshly caught, or obtained from a fish-holding tank, and were filleted immediately after killing. There was no significant difference in results between the pre-rigor and post-rigor extracts.

After mincing in a chilled meat grinder, the flesh was mixed with an equal weight of cold water (2°C), and stirred occasionally for 1 to 2 hr (Dingle *et al.*, 1955). Extraction overnight yielded more protein, but electrophoretic analysis showed that the composition of the extract remained unaltered. The resulting slurry was centrifuged at 1400 × *g* to remove debris and the supernate used as the starting material for the fractionations.

Free boundary electrophoresis was conducted at 1.6°C in a Spinco Model H apparatus, and sedimentation analysis in a Spinco Model E ultracentrifuge. In both cases, samples were first dialyzed against 0.05*M* KCl containing KH_2PO_4 adjusted to the appropriate pH and to total ionic concentration ($\Gamma/2$) of 0.10 by addition of KOH. Before the analyses, the dialyzed samples were centrifuged at 25,000 × *g* for 10 min. With extracts, this treatment yielded a small residue and an opalescent supernate. In the case of the fractions soluble in zinc acetate, the residues were negligible, and the supernates were clear. Amino acid analyses were made with a Spinco Model MS Amino Acid Analyzer on samples that had been hydrolyzed by boiling with 6*N* HCl for 24 hr. Protein was determined by the biuret procedure of Snow (1950).

DEAE-cellulose, Type 40, from the Brown Company of Berlin, New Hampshire, U.S.A., was used for chromatographic fractionation. This material was suspended in water, brought to pH 7 with concentrated KH_2PO_4 solution, and the fines were decanted. After filtering, the cellulose was washed with 0.01*M* KH_2PO_4 adjusted to pH 7 with KOH, ("KH_2PO_4 buffer, pH 7"), then suspended in the same reagent for loading into the column. Equilibration was allowed to proceed overnight. The column (27 cm long by 2.2 cm internal diameter) was fitted with a water jacket, and during elution was cooled to approximately 7°C.

Concentration of protein solutions was achieved when necessary by dialyzing against "Carbowax" (Type 20 M polypropylene glycol) obtained from the Carbide Chemicals Company, Montreal. The powder was loaded into Visking cellulose sacs which in turn were suspended in the protein solutions contained in graduated cylinders. Regular Visking tubing was used; the special dialysis tubing was found to be permeable to a portion of the Carbowax.

Reagent-grade zinc acetate was made up to 1*M* and diluted as required. The pH of this solution was approximately 6.0; any attempt to raise the pH by addition of KOH resulted in the formation of a precipitate, so the solution was used without adjustment.

Electrophoresis of Extracts

Typical patterns for water extracts of cod and haddock muscle are shown in Fig. 1. The numbering of the peaks in the cod extract corresponds with that given by Connell (1953); in the case of haddock the numbering is the result of an attempt to correlate the peaks with those of cod according to mobility, but should be considered to be arbitrary. It will be noted that some components in the haddock extract were more electropositive than any found in the cod extracts.

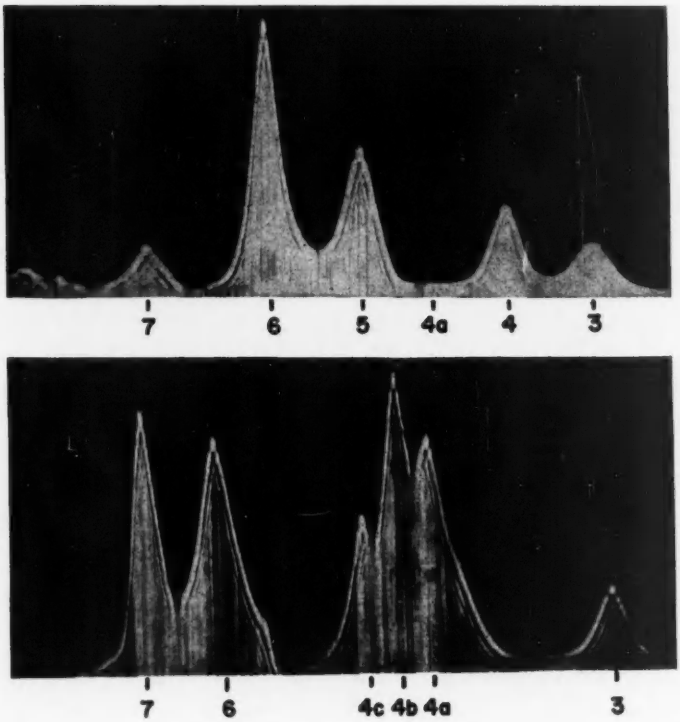

Fig. 1. Electrophoretic patterns (ascending) of aqueous extracts of fish muscle.
Solvent: 0.05*M* KCl + KH_2PO_4 buffer, total $\Gamma/2 = 0.10$. Migration to the right.
Top: Post-rigor cod, 1.59 mg N/ml, pH 6.54, 7.13 volt/cm, after 320 min.
Bottom: Post-rigor haddock, 2.42 mg N/ml, pH 6.72, 7.10 volt/cm, after 320 min.

Precipitation Curve

To 5-ml aliquots of extract in centrifuge tubes were added cold zinc acetate solution, water, and in some experiments, NaCl solution, to give total final volumes of 10 ml at the desired concentrations of zinc ionic concentration. The

total amount of protein N in the mixture was approximately 14 mg. After mixing and standing in the cold for 20 min, the mixtures were centrifuged for 5 min at 1500 × *g* and the supernates analyzed for protein N. Typical curves for cod are shown in Fig. 2. These were qualitatively reproducible, and there was generally a suggestion of stepwise precipitation. Under these conditions, approximately 35% of the original protein remained soluble up to a zinc acetate concentration of 0.10*M*. It was also found that an increase of ionic strength by addition of NaCl resulted in a shift of the precipitation curve to higher zinc acetate concentrations. It was not possible to vary greatly the pH of the precipitation. There was a tendency for zinc hydroxide to precipitate above pH 6.0, while below this value some protein was precipitated even in the absence of zinc. The final pH of the mixtures was 5.9 to 6.0.

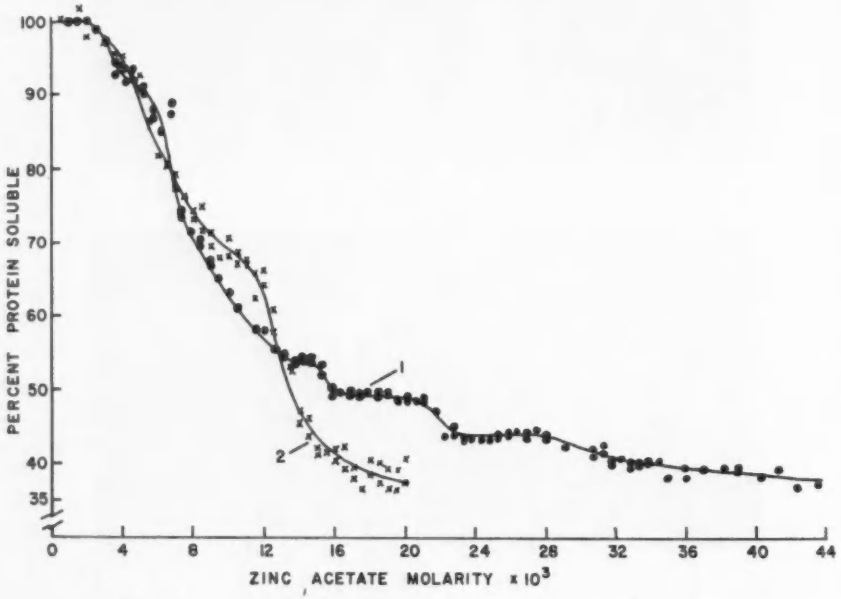

FIG. 2. Precipitation of proteins of aqueous extracts of cod muscle with zinc acetate.
Curve 1: Extract A in water.
Curve 2: Extract B in 0.1*M* NaCl.
Temperature, 5°C; pH 6.2.

FRACTIONATION

In some preliminary work with cod muscle extracts, precipitates formed between several stages of the zinc acetate concentration were collected. These could generally be redissolved with small residues by stirring for several hours in the cold with 0.1*M* disodium ethylenediamine tetra-acetate (EDTA), pH 8.0. Sodium citrate (0.1*M*, pH 9) was less effective, while 0.1*M* glycine was found to be quite unsatisfactory. According to electrophoretic mobilities the

fractions precipitated between 0 and 0.11*M* zinc acetate, and also between 0.024 and 0.030*M* zinc acetate, consisted largely of component 6 (see Fig. 1, top), while intermediate fractions were enriched in component 5. The first-mentioned fraction also possessed an enhanced adenosinetriphosphate–creatine kinase activity. These results indicated a selective precipitation by zinc acetate, but this work has not been carried further.

Fraction Soluble in 0.1*M* Zinc Acetate

As already mentioned, approximately 35% of the original protein of water extracts of cod muscle remained soluble after 20 min in the presence of 0.1*M* zinc acetate. On standing in the cold for 18 hr, however, a further small precipitation occurred (Fig. 3). When an attempt was made to dialyze the supernate against the electrophoresis buffer, a heavy precipitate formed in the sacs. This was at first thought to be due to the formation of zinc phosphate, but it was found that a further heavy precipitation of protein had occurred. Tests showed that if the supernate obtained from the 20-min precipitation with 0.1*M* zinc acetate was treated with one-tenth volume of KH_2PO_4 buffer, pH 6.6, this precipitation

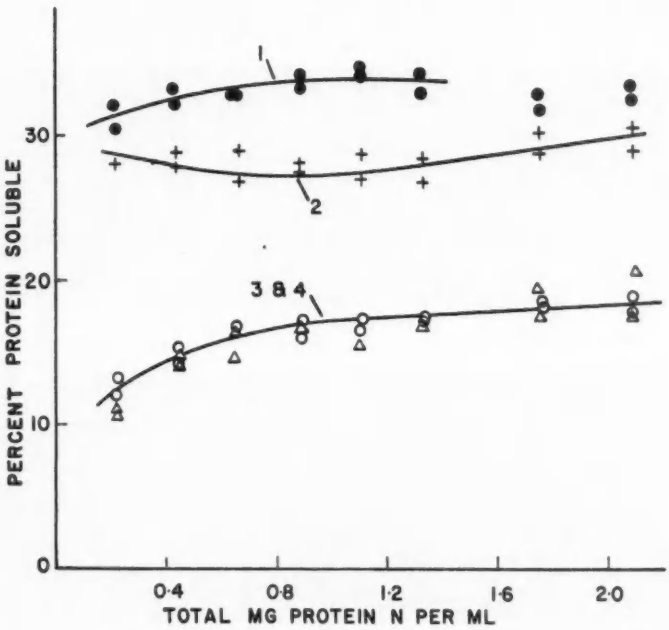

Fig. 3. Precipitation of proteins of an aqueous extract of cod muscle.
Curve 1: Precipitation with zinc acetate, separated after 20 min.
Curve 2: Same as curve 1, separated after 18 hr.
Curve 3: Precipitation with zinc acetate then with potassium phosphate, separated after 20 min.
Curve 4: Same as curve 3, separated after 18 hr.
Temperature, 2°C; zinc acetate, 0.1*M*; KH_2PO_4 buffer, pH 6.6, 0.1*M*.

occurred immediately and did not increase with time (Fig. 3, curves 3 and 4). Attempts were made to forestall further precipitation after addition of the zinc acetate to the extract by adding 0.1*M* EDTA to remove excess zinc ion. This, however, resulted in a heavy precipitation similar to that caused by the phosphate buffer. Electrophoresis showed that the supernates remaining after treatment of the 0.1*M* zinc acetate supernate with phosphate or with EDTA were similar. Attempts to redissolve the precipitates have not been successful, and their natures remain uncertain.

The zinc-acetate-soluble fraction was routinely prepared by adding to a water extract of muscle one-tenth volume of cold 0.1*M* zinc acetate, centrifuging at 1200 × g for 20 min, adding to the supernate one-tenth of its volume of cold 1.0*M* KH_2PO_4 buffer, pH 6.6, and centrifuging again as before. These operations were performed in a cold room at 2°C. The resulting supernate was clear and had a slight yellow colour. Approximately 18% of the original protein remained soluble after this treatment.

Electrophoretic analysis was carried out on fractions prepared from cod and haddock muscle after the fractions had been suitably concentrated by dialysis against Carbowax. Results of typical runs are given in Fig. 4. The mobilities

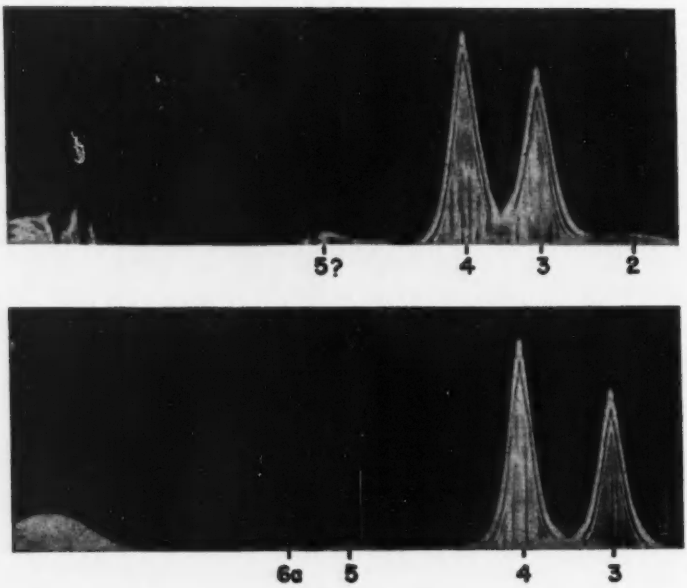

FIG. 4. Electrophoretic patterns (ascending) of fractions of aqueous extracts of fish muscle soluble in 0.1*M* zinc acetate + 0.1*M* KH_2PO_4 buffer, pH 6.6. Solvent: 0.05*M* KCl + KH_2PO_4 buffer, total $\Gamma/2 = 0.10$. Migration to the right.
Top: Post-rigor cod, 1.10 mg N/ml, pH 7.76, 5.31 volt/cm, after 370 min.
Bottom: Post-rigor haddock, 0.90 mg N/ml, pH 7.70, 709 volt/cm, after 315 min.

of the two main peaks in the cod fraction indicated that these two components were identical with components 3 and 4 of the original extract. Moreover, the mobilities of the two main components of the haddock fraction agreed closely with those of the cod fraction at comparable pH. This is shown in Fig. 5, in which the dependence of mobility on pH is given for the cod fraction components.

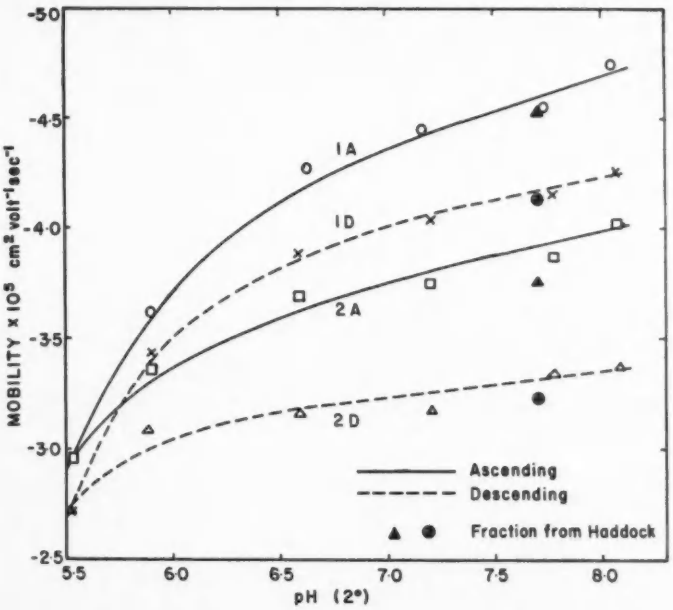

FIG. 5. Dependence on pH of the electrophoretic mobilities of the main components of the zinc-acetate-soluble fraction from an aqueous extract of cod muscle.
Solvent: 0.05*M* KCl + KH_2PO_4 buffer, total $\Gamma/2 = 0.10$; temperature, 1.6°C, field strength, 5.3 to 6.3 volt/cm; protein concentration, 1.1 mg N/ml.
Curves 1A and 1D: Component 3.
Curves 2A and 2D: Component 4.
Also shown are results of a single run on an analogous fraction from haddock muscle.

The result of an ultracentrifuge run on a fraction prepared from cod muscle is given in Fig. 6. In this case the sample contained some Carbowax which had diffused through the special Visking dialysis tubing that had been used. The two main components discernible had sedimentation constants (at the conditions of the run) of 2.5 and 1.1, and 2.7 and 1.2, at approximate protein concentrations of 1.0 and 0.5 mg N/ml respectively.

In an attempt to separate the two main components in the cod fraction, mercuric acetate was added to a concentration of 0.005*M*. A further precipitation of protein occurred, but electrophoresis of the concentrated supernate revealed that the composition had not been significantly changed.

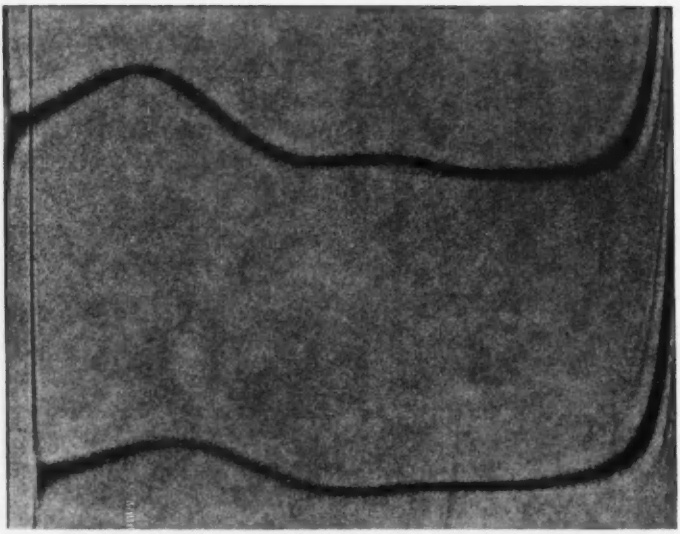

FIG. 6. Ultracentrifuge pattern of the zinc acetate-soluble fraction from an aqueous extract of cod muscle.
Solvent: 0.05*M* KCl + KH_2PO_4 buffer, pH 6.6, total $\Gamma/2 = 0.10$. Temperature, 0°C, after 208 min at 59,780 r.p.m. Sedimentation to the right.
Top: 1.0 mg N/ml.
Bottom: 0.5 mg N/ml.

In another attempt, a concentrated fraction from cod was applied to a DEAE-cellulose column. Twenty millilitres of solution containing 67 mg of protein N was applied. Elution with 0.05*M* KH_2PO_4 buffer, pH 7.0, yielded only two components comprising 25% of the added protein. Addition of KCl to the eluting solution extracted further protein, and in three subsequent runs linear gradient elution up to 0.7*M* KCl was used. The ultraviolet absorption of the eluted fractions was measured at 250 and 280 mμ. The chromatograms so determined were qualitatively reproducible and a typical one is shown in Fig. 7. Recovery from the column was, however, only 65 to 67%.

Chromatographic fractions II, III, and IV were concentrated with Carbowax, and analyzed by electrophoresis. Only negligible material remained in fraction III, due either to a leak in the dialysis sac, or to a depolymerization having occurred. The patterns obtained for the other two fractions are shown in Fig. 8. Fraction II contained most of the impurities of the original fraction. Fraction IV was found to consist almost entirely of electrophoretic components 3 and 4, according to their mobilities, and by measurement of the areas of the peaks of the electrophoretic pattern their distribution was: component 3, 58%; component 4, 40%; other, 2%. Thus, while chromatography on DEAE-cellulose under the present conditions failed to give the desired separation, the electrochemical properties of the proteins appear to have remained unchanged.

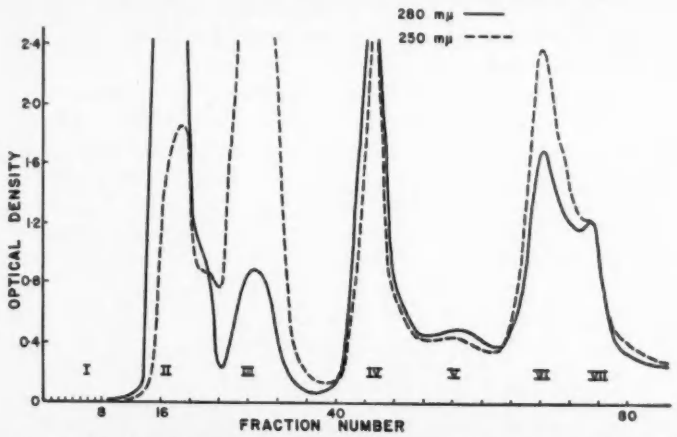

FIG. 7. DEAE-cellulose chromatogram of zinc-acetate-soluble fraction of aqueous extract of cod muscle.

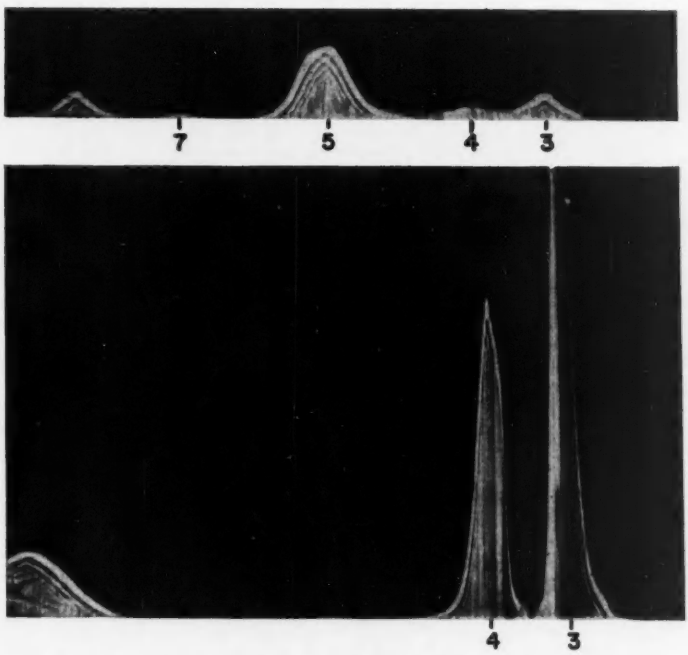

FIG. 8. Electrophoretic patterns (ascending) of DEAE-cellulose chromatography fractions of zinc-acetate-soluble proteins from an aqueous extract of cod muscle.
Solvent: 0.05*M* KCl + KH_2PO_4 buffer, total $\Gamma/2 = 0.10$. Migration to the right.
Top: Fraction II (see Fig. 7) 0.42 mg N/ml, pH 6.6, 5.96 volt/cm, after 345 min.
Bottom: Fraction IV (see Fig. 7) 1.63 mg N/ml, pH 6.6, 5.97 volt/cm, after 342 min.

The ultraviolet absorption spectra were determined with a Beckman DK-2 recording spectrophotometer for several of the chromatography fractions, and are reproduced in Fig. 9. Fraction III had a maximum absorption at 249 mμ, suggestive of an inosine derivative. The main fraction, IV, (electrophoretic components 3 and 4 in cod) had a spectrum unusual for a protein, and is reminiscent of that reported by Jebsen and Hamoir (1958) for a component of plaice myogen. The maxima at 254, 259, and 265 mμ appeared to correspond with those of phenylalanine at 252, 257, and 263 mμ (Fromageot and Schnek, 1950). Amino acid analysis of an acid hydrolysate of fraction IV confirmed the presence of an unusually large amount of phenylalanine (11.8% by weight) (Fig. 10). This would account for about 46% of the absorption at 259 mμ, and a further 33% would be due to the relatively small amounts of tyrosine and tryptophan also present.

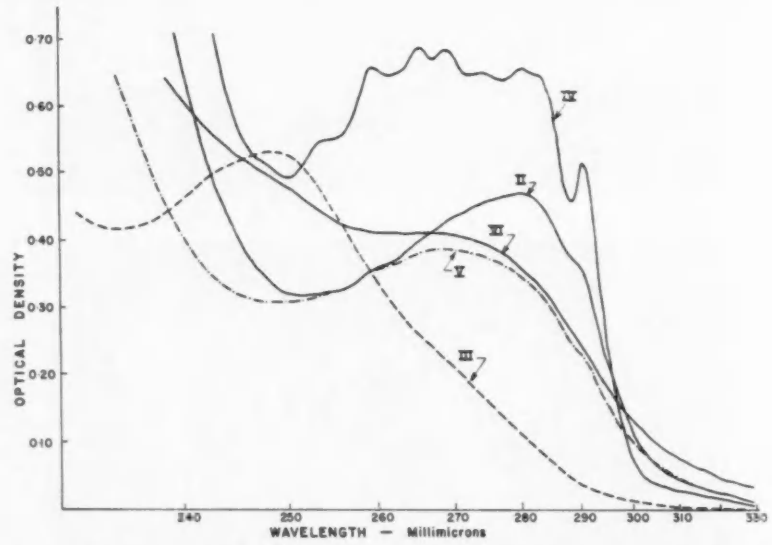

FIG. 9. Ultraviolet absorption spectra of DEAE-cellulose chromatography fractions of zinc-acetate-soluble proteins from an aqueous extract of cod muscle. Numbers correspond to fractions indicated in Fig. 7, pH 7.0.

EFFECT OF STARVATION

Many electrophoretic analyses carried out in the course of other studies on low ionic strength extracts of cod muscle yielded patterns closely resembling that in Fig. 1, top. In certain cases, however, it was noted that the proportion of component 4 was greatly increased, while that of component 3 was somewhat decreased. It appeared that this might be related to environment temperature which in turn was related to the feeding of the fish. To test this, extracts were made from fillets of two cod of nearly equal size, one of which had been kept in a

tank at 6°C and was feeding freely, and the other in a tank at 2.5°C and which had refused to feed. Both had been held in the tanks for at least 2 weeks. The electrophoretic patterns of the water extracts are shown in Fig. 11, and the relative proportions of the several components determined by measurement of peak areas are given in Table I.

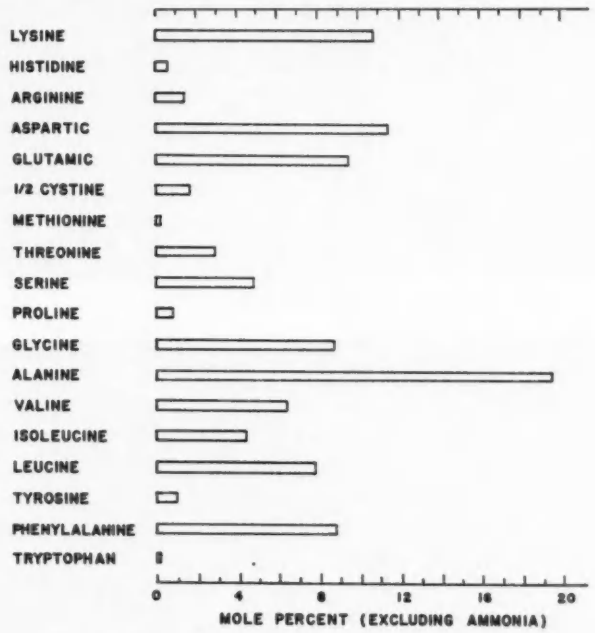

FIG. 10. Amino acid composition of zinc-acetate-soluble proteins from an aqueous extract of cod muscle.

TABLE I. Composition of aqueous extracts of muscle of starved and feeding cod.

Electrophoretic peak number	Percentage of total electrophoretic pattern area			
	Starved cod		Feeding cod	
	Ascending	Descending	Ascending	Descending
1	7.1	4.5	6.5	7.1
2	5.7	5.0	5.1	4.4
3	8.1	7.6	8.9	9.0
4	21.2	24.9	15.0	16.5
4a	2.6	2.5	2.8	2.9
5	16.4	16.7	15.4	14.6
5a	3.1	{31.4}	6.3	5.8
6	28.6		28.5	29.2
7	5.1	7.0	8.9	10.0

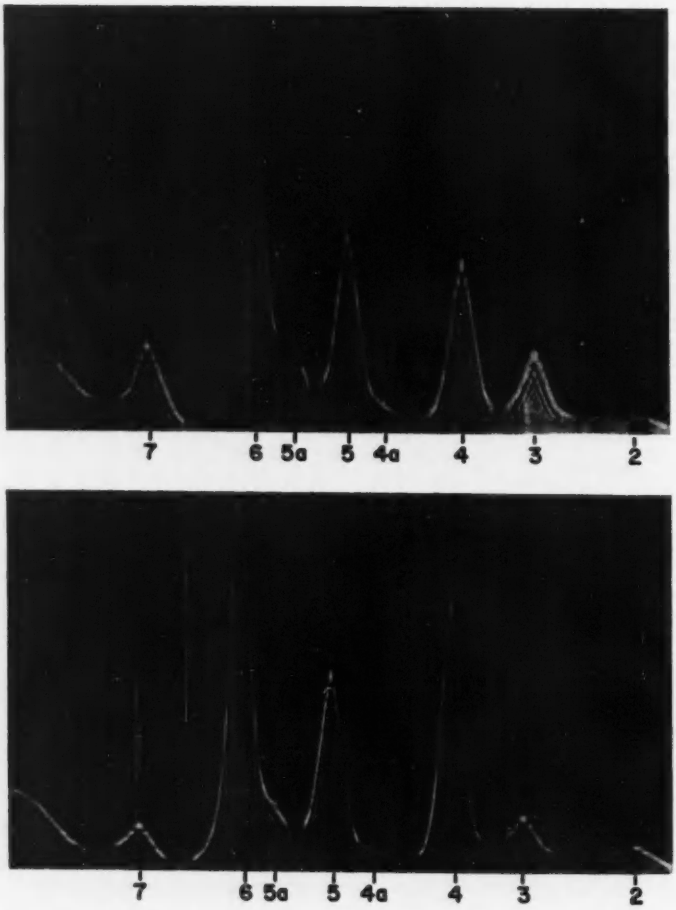

FIG. 11. Electrophoretic patterns (ascending) of aqueous extracts of muscles of normal and starved cod.

Solvent: 0.05*M* KCl + KH_2PO_4 buffer, total $\Gamma/2 = 0.10$; pH 6.61; 7.4 volt/cm. Migration to the right.

Top: Normal cod, 2.13 mg N/ml.

Bottom: Starved cod, 2.06 mg N/ml.

In our experience, the proportion of component 4 in aqueous extracts of muscle of post-rigor commercial cod usually lay in the range 14 to 18%, and of component 6 in the range 28 to 30%. An enhanced amount of component 4 (greater than 20%) has, however, occasionally been found in muscle extracts of fish caught during the winter months. A variation in amount of the component has also been observed in extracts made from adjacent portions of the same fillet,

both pre-rigor and post-rigor, of a cod held in the 2.5°C tank. While the cause of these variations is not known, the variations appear to be real, since duplicate electrophoretic analyses on one extract were indistinguishable.

DISCUSSION

Henrotte (1955) and Hamoir (1957) have reported the isolation from carp myogen (water extract) of a crystalline component that precipitates with ammonium sulphate at very high salt concentration, contains about 15% phenylalanine, and no tyrosine and tryptophan. Jebsen and Hamoir (1958), by means of preparative electrophoresis, isolated a protein from a fraction precipitating from plaice myogen with ammonium sulphate between 90 and 100% saturation. Like the carp component, this protein had a corrected sedimentation constant of 1.4 to 1.5 S, and the same unusual aromatic amino acid composition. The electrophoretic descending mobilities differed, however, being -6.5×10^{-5} $cm^2volt^{-1}sec^{-1}$ for plaice ($\Gamma/2 = 0.05$, pH 7.5) and -3.2×10^{-5} $cm^2volt^{-1}sec^{-1}$ for carp ($\Gamma/2 = 0.075$, pH 7.3). The latter value agrees closely with those found for component 4 in the cod and haddock zinc-acetate fractions under nearly the same conditions, but one cannot yet be certain which of our two components corresponds with the nearly pure one isolated by Jebsen and Hamoir. Similar components can, however, be expected to occur in extracts of muscle of other fishes.

While the recovery of protein from the DEAE-cellulose column was incomplete, the protein eluted apparently was not damaged by the procedure. Although this and similar techniques will undoubtedly be very widely used in the future for analysis and isolation of proteins, the present work suggests that it may be worth considering precipitation with metal ions as a possible clean-cut method of effecting preliminary simplifications of mixtures.

Several questions remain unresolved. For example, why is protein precipitated when KH_2PO_4 or EDTA are added to the extracts containing zinc ion? It is not known whether the final fractions contain bound zinc ion, or whether these proteins originally contained zinc or some other metal ion. Finally, the physiological significance of these proteins has not been determined, although the effect of starvation and/or low temperature is intriguing.

ACKNOWLEDGMENT

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Conversion of the Free Fatty Acids of Cod Oil to Methyl Esters in situ[1]

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ABSTRACT

The application of 2,2-dimethoxypropane to the in situ conversion of the free fatty acids of cod oil to methyl esters is successful in reducing the free fatty acid content to the order of 1%. This material, in the presence of a suitable acid catalyst, serves both as a water scavenger and a source of methanol for the esterification. Of the catalysts examined, methanolic HCl gives the best results. Purification procedures giving a stable product are outlined.

The cod oils produced on the Atlantic coast of Canada, particularly those produced by "sun-rotting", may contain up to 30% free fatty acids (Bailey *et al.*, 1952a) expressed as oleic acid (Bailey *et al.*, 1952b). However, large quantities of oil are available, through segregation of materials purchased at plants, with free fatty acid (FFA) content of 12% or less. Refining of these better quality cod oils through classical alkali refining is feasible, but the losses tend to be high and the recovered alkali foots of little value.

Esterification of the FFA in situ would be an attractive means of improving the quality and marketability of these oils. The use of glycerol in this type of reaction as applied to various types of oils has been the subject of much interest and has recently been reviewed by Cruz and Romero (1958), while the merits of the reaction have been discussed by Anderson (1953a). The use of glycerol and similar non-volatile alcohols requires high temperatures and/or relatively large amounts of strong acid catalysts, and relatively high costs for plant equipment. The economics are such that these processes have been applied only to high-cost oils, or in periods of acute fat shortages (Anderson, 1953a; Santelli, 1951).

The conversion of the FFA to esters of the lower alcohols by conventional procedures has also been applied (Anderson, 1953a), but presents considerable difficulties owing to the competing reactions of esterification (a) and interesterification (b):

(a) $R{-}CO_2H + R'OH \longrightarrow R{-}CO_2{-}R' + H_2O$

(b) $$\begin{array}{l} R{-}CO_2{-}CH_2 \\ \quad\quad | \\ R{-}CO_2{-}CH \\ \quad\quad | \\ R{-}CO_2{-}CH_2 \end{array} + 3\ R'OH \longrightarrow 3\ R{-}CO_2{-}R' + CHOH\ (CH_2OH)_2$$

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The water liberated in reaction (a) prevents the reaction from proceeding to completion, and if excess alcohol is added to force the reaction toward completion the overall conversion to esters increases due to reaction (b). The latter reaction takes place stepwise, so that considerable amounts of mono- and diglycerides are formed as well. The removal of the water formed during esterification is therefore the key factor in esterification of FFA of oils in situ.

This difficulty has been overcome in one procedure by converting the FFA under anhydrous conditions to the sodium salts and treating the mixture of oil and soap with dimethyl or diethyl sulphate in the presence of a buffering alkali which absorbs the sulphuric acid liberated (Bradshaw, 1946). The FFA of greases or tallows may thus be reduced from 22 to 0.5%. The reaction is relatively simple but requires stepwise addition of materials and careful temperature control.

The introduction of acetone dimethyl acetal (2,2-dimethoxypropane) (DMP) for the preparation of methyl esters of fatty acids (Lorette and Brown, 1959; Brown and Lorette, 1961) suggested that the problem of removing the water formed during the esterification reaction could be solved, since in this reaction (c):

$$\text{(c)}\quad H_2O + (CH_3)_2C(OCH_3)_2 \longrightarrow 2\ CH_3OH + CH_3{-}CO{-}CH_3$$

the reagent may serve both as a source of methanol (MeOH) and a water scavenger. Further advantages were offered in that the reaction requires only simple equipment and proceeds at room temperature. Preliminary results indicated that this reaction could be successfully applied to the esterification of the FFA in cod oil and experiments were therefore carried out to determine the nature and amount of catalyst necessary, the least amount of reagent which could be employed, operating conditions, and the necessary purification of the product to ensure optimal quality and stability.

The experiments carried out in the present study were based on the possible use of this reaction in oil plants with limited equipment and personnel. Consequently the intended optimal simplification of the reaction for such circumstances would be one that would require only a covered vessel, an agitator, little or no attention during reaction, and a reaction period suited to one-shift plant operation. Similar considerations dictated the use of the minimum of reagent and simple purification steps, employing equipment readily available.

EXPERIMENTAL

Materials

Cod oil was obtained through the courtesy of Fishery Products Ltd., St. John's, Newfoundland. The FFA content was determined (as oleic acid) by the procedure given in the Official and Tentative Methods of the American Oil Chemists' Society, revised to 1961, and was found to be 10.12%. The water content was estimated by azeotropic distillation with toluene to lie between 0.3 and 0.4% w/w. Monoglycerides were determined as 4.76% by the procedure of Pohle and Mehlenbacher (1950). The reagent, 2,2-dimethoxypropane of

TABLE I. Influence of acid catalyst concentration on percentage FFA of 100 g cod oil treated with 0.041 mole DMP.

Catalyst:	Hydrogen chloride			*p*-Toluenesulphonic acid				Dimethyl sulphate		
Equivalents:	0.0057	0.0029	0.0014	0.0058	0.0029	0.0014	0.0006	0.0106	0.0054	0.0025
Vol. methanolic HCl added, ml:	1.3	0.65	0.32	0.5	0.5	0.5	0.5	0.5	0.5	0.5
	%	%	%	%	%	%	%	%	%	%
FFA after:										
24 hours	1.41	6.37	9.35	1.70	1.85	2.66	7.77	3.84	9.25	9.98
48 hours	...	...	...	1.61	1.81	2.18	6.58	3.13	8.45	9.90
4 days	1.50	5.34	9.10	...	...	...	...	...	...	...
5 days	...	...	...	2.57	2.03	2.14	3.68	2.40	4.16	10.01

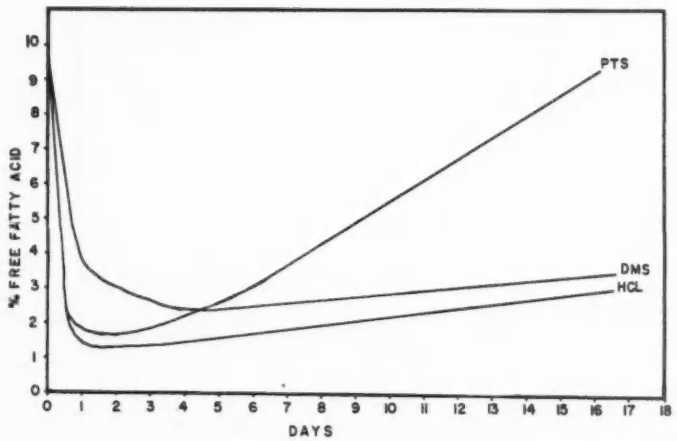

Fig. 1. Long-term stability of esterification reaction mixtures with *p*-toluenesulphonic acid (PTS), dimethyl sulphate (DMS) and methanolic HCl as acid catalysts, respectively 0.0058, 0.0106, and 0.0057 eq/100 g oil.

98% minimum purity, was supplied through the courtesy of Dr N. B. Lorette, Dow Chemical Co., Freeport, Texas. Reagent-grade MeOH was used throughout this study, while the acid catalysts employed were Eastman reagent *p*-toluenesulphonic acid, technical dimethyl sulphate, and dry HCl gas passed into chilled MeOH until suitable concentrations were reached.

COMPARISON OF VARIOUS ACID CATALYSTS AND STABILITY OF REACTION MIXTURES

Cod oil (100-g lots, approximately 0.035 mole FFA, calculated as oleic) was weighed into 250-ml Erlenmeyer flasks (ground-glass stoppers) containing teflon-coated magnetic stirring bars. To each, while gently stirring, were added DMP (5.0 ml, 0.041 mole) and catalyst and MeOH as indicated in Table I. The stronger acid concentration mixtures darkened immediately, excepting in the case of the *p*-toluenesulphonic acid, which did not dissolve for several minutes,

delaying the formation of colour. Stirring was continued for 6 hours of the first 24-hour period, but on subsequent days was restricted to a few minutes prior to removal of each sample for examination. The FFA values after 24 hours and several days are listed in Table I. The three highest acid concentration mixtures were examined at later times with the results indicated in Fig. 1.

Influence of HCl Concentration on the Reaction

Cod oil (100-g lots) was treated as described above with DMP (3.0 ml, 0.025 mole) and methanolic HCl solutions (1.3, 1.3, 1.5 and 1.5 ml) containing respectively 0.0022, 0.0057, 0.0102 and 0.0120 eq HCl. The FFA values of the reaction mixtures at various times are illustrated in Fig. 2.

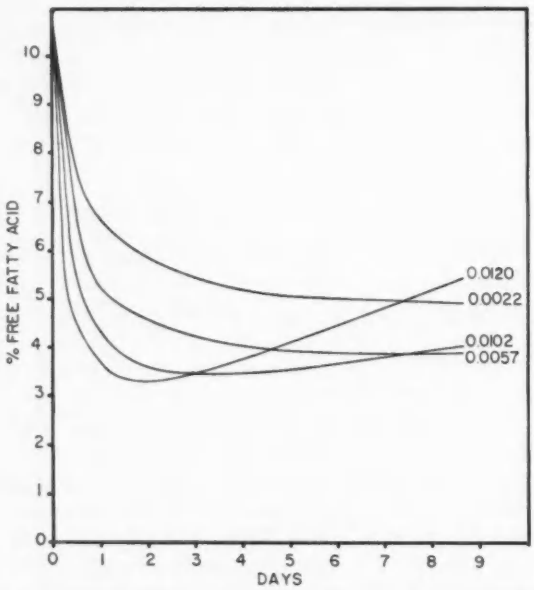

Fig. 2. Course of reactions of 100 g cod oil with 0.025 mole of DMP and varying amounts (eq) of HCl.

Examination of Effect of Lesser Amounts of 2,2-Dimethoxypropane

Cod oil (100-g lots) was treated as before with DMP (5.0, 4.0 and 3.0 ml, respectively 0.041, 0.033 and 0.025 mole) in the presence of MeOH, added as methanolic HCl (1.3 ml, estimated at 0.03 mole MeOH and 0.0057 eq HCl). The water in the oil was estimated not to exceed 0.022 mole and the water liberated during the esterification as 0.035 mole. The results are summarized in Table II.

In a further experiment the same procedure was followed using lesser amounts of DMP (0.025, 0.016 and 0.008 mole respectively) with a higher concentration of HCl in MeOH (1.5 ml, estimated to contain 0.03 mole MeOH and 0.0102 eq HCl). The results are summarized in Table II and Fig. 3.

TABLE II. Influence of the amount of DMP on percentage FFA of 100 g cod oil in the presence of MeOH.

DMP, moles:	0.041	0.033	0.025	0.025	0.016	0.008
Methanolic HCl, ml:	1.3	1.3	1.3	1.5	1.5	1.5
HCl, equivalents:	0.0057	0.0057	0.0057	0.0102	0.0102	0.0102
	%	%	%	%	%	%
FFA after:						
24 hours	2.65	3.42	5.16	4.28	5.56	7.01
48 hours	2.01	2.81	4.58	3.61	5.00	6.50
96 hours	1.62	2.25	3.86	...	...	...
120 hours	...	...	...	3.52	4.77	6.63

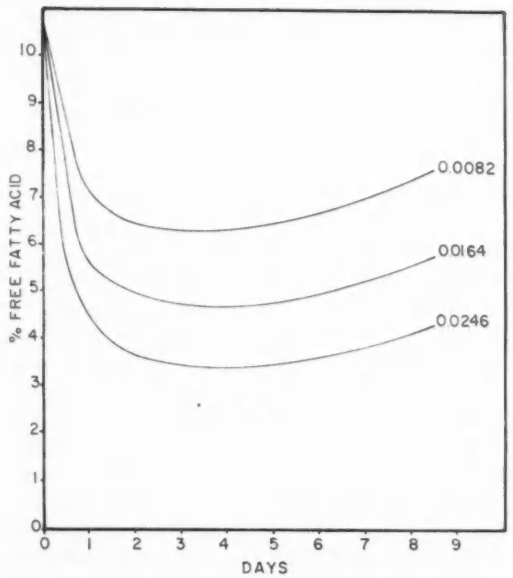

FIG. 3. Typical family of curves obtained with 100 g cod oil, varying amounts (moles) of DMP, and fixed amount of HCl and MeOH.

INFLUENCE OF METHANOL ON RATE OF REACTION

Cod oil (100-g lots) was treated with DMP (5.0 ml, 0.041 mole) and dimethyl sulphate (0.60 ml, 0.0128 eq). Two lots received added MeOH (0.32 ml and 0.64 ml, respectively 0.008 and 0.016 mole) while a third lot received no MeOH. After 5 days the FFA percentages were found to be respectively 1.69, 1.71 and 1.90, and after 11 days 1.45, 1.47 and 1.78.

TREATMENT WITH FILTER AIDS

A dimethyl sulphate reaction mixture (100-g lots) was stirred with varying amounts of different filter aids for periods of up to 8 hours. Over this time

stirring was for short intermittent periods only. Samples were removed after 1, 24 and 48 hours, the filter aid was centrifuged out, and the clear oil stored in screw-cap vials for immediate and later FFA determinations. The results are presented in Table III.

TABLE III. Influence of varying amounts of some filter aids and of treatment times on stabilization of a dimethyl sulphate reaction product.

Material	Percentage (w/w)	Treatement time, hours	Percentage free fatty acid after storage for		
			0 day	18 days	30 days
Bentonite	0.5	1	1.80	2.20	2.60
Celkote	0.5	1	1.76	2.08	2.49
Micro-Cel	0.5	1	1.74	1.95	2.32
	0.5	48	1.29	1.47	1.80
	1.0	1	1.52	1.67	1.78
	1.0	24	1.16	1.17	1.57
	1.0	48	0.98	1.26	...
	2.0	1	1.21	1.24	1.31
	2.0	24	1.00	0.89	0.89
	2.0	48	0.65	...	0.76
	3.0	1	1.01	0.96	1.11
	3.0	24	0.63	0.63	0.70
	3.0	48	0.68	...	0.64
None	...	...	1.78	2.29	2.72

LARGE-SCALE REACTIONS AND PURIFICATION OF ESTERIFIED OILS

Experiment A. Cod oil (5.1 kg) was stirred vigorously while adding *p*-toluenesulphonic acid (51 g, 0.3 eq), DMP (250 ml, 2.04 moles) and MeOH (10 ml, 0.3 mole). After 8 hours, stirring was discontinued and after 24 hours the FFA had fallen to 1.85%. The product developed an offensive sulphurous odour on treatment with bentonite (0.5%), and no further investigations were undertaken.

Experiment B. Cod oil (14.5 kg) was stirred vigorously in a 5-gallon (19-l) bottle while dimethyl sulphate (72 ml, 1.52 eq) and DMP (720 ml, 5.87 moles) were added. The mixture was stirred continuously for 24 hours, FFA then being 3.19%, and occasionally over a further 4 days, resulting in a final FFA of 2.05%. Part of the product (5 kg) was removed and stirred for 8 hours with Johns-Manville Micro-Cel (25 g, 0.5% w/w). After a total of 24 hours this mixture was again stirred and filtered by suction. The bulk of the oil layer was stirred with tap water (3 l) for 1.5 hours. After a settling period of 24 hours, part of the oil layer (4.3 kg) was removed and treated for 24 hours with Micro-Cel as described above. The remainder of the oil layer was clarified in a Sharples Super Centrifuge, and a portion (2 kg) treated with Micro-Cel as above. The various products were stored in glass containers and examined from time to time for FFA. The results are presented in Table IV.

TABLE IV. Percentage FFA of esterified cod oils purified by various procedures, when freshly prepared, and after storage.

Experiment:	B			C			D		
Catalyst:	Dimethyl sulphate			Methanolic HCl			Methanolic HCl		
FFA values:	Orig.	Final		Orig.	Final		Orig.	Final	
	%	%	*days*	%	%	*days*	%	%	*days*
Product treatment:									
Micro-Cel only	1.51	3.83	81	1.45	1.31	73	3.07	3.02	38
Washed, settled and treated with Micro-Cel	1.27	2.88	81	0.73	0.71	73	2.69	2.77	38
Washed, settled and clarified	2.12	3.33	70	1.96	2.03	70	4.29	4.36	38
Washed, settled, clarified and treated with Micro-Cel	1.37	1.51	70	1.38	1.34	70	2.92*	2.94	38
							3.39†	3.44	38

*1% Micro-Cel.
†0.5% Micro-Cel.

Experiment C. Cod oil (14.8 kg) was similarly treated with DMP (700 ml, 5.70 moles) and methanolic HCl (190 ml, 0.84 eq HCl). After stirring for 24 hours the FFA was found to be 2.77%, and after a further 2 days it had fallen to 2.04%. The further treatment followed that outlined above for the dimethyl sulphate catalysed reaction, except that the washed oil layer sample was treated with Micro-Cel (0.5% w/w) for 24 hours, followed by addition of a further 0.5% and treatment for an additional 24 hours prior to filtration. The results are summarized in Table IV.

Experiment D. Cod oil (3.0 kg) was treated as above with a lesser proportion of DMP (75 ml, 0.61 mole) and methanolic HCl (45 ml, 0.306 eq). After 2 days the FFA was 4.29%, and after 5 days 4.28%. To part of the reaction mixture (900 g) was added 0.5% Micro-Cel and after 24 hours a further 0.5%. After a total of 48 hours the mixture was filtered. The balance of the reaction mixture was stirred with tap water (1 l) for 1 hour and allowed to settle for 24 hours. Part of the oil layer was then decanted and similarly treated with Micro-Cel. The balance was clarified by centrifugation and part of the clarified material was treated as above with 1% Micro-Cel in two 24-hour stages, while the remainder was treated with only 0.5% for 48 hours. The results are summarized in Table IV.

DISCUSSION

Of the acid catalysts chosen for study, hydrogen chloride and *p*-toluenesulphonic acid were employed by Lorette and Brown (1959), while dimethyl sulphate was selected as a convenient means of introducing sulphuric acid into the reaction mixture. The hydrolysis of the latter catalyst may under these conditions not be complete, but all the catalysts may ultimately be partially combined, since the FFA values may be found to be of the same order as those which would be given by the catalyst acid itself, yet are not reduced by washing,

as would be expected if they were all mineral acid. The data in Table I and Fig. 2 indicate that there is for each catalyst a limiting catalyst concentration below which the esterification reaction does not proceed very rapidly. The lowest FFA level is also not necessarily reached with low concentrations of catalyst. The latter effect may be due to the competing acid-catalysed reactions of esterification, and decomposition of the DMP to isopropenyl methyl ether and MeOH, where the latter reaction destroys the reagent before the esterification reaction can be completed; or to loss of acid catalyst as described above.

With all acid catalysts (Table I, Fig. 2), the lowest FFA values are obtained with the highest concentration of acid catalyst.

While *p*-toluenesulphonic acid was the most active catalyst, effective even in low concentrations, it was slow to dissolve in the cod oil. Other disadvantages were the rapid increase in FFA value of the reaction mixture on standing (Fig. 1), the development of objectionable odour, and the probable difficulty in removing this acid by washing procedures. The dimethyl sulphate did not seem as active as the other catalysts, and gave a somewhat darker and less stable product. The possibility of sulphation of ethylenic double bonds must also be considered. The methanolic HCl solution was found to be particularly satisfactory as a catalyst from the points of view of rapid reaction, low free fatty acid value at minimum, slow increase of free fatty acid value after minimum, ease of purification, and stability of purified product.

A comparison of Table I with the experimental details outlined above for large-scale reactions indicates that even with continuous agitation the large-scale reactions were somewhat slower than the small-scale reactions. The reason for this is not clear, although the fact that the large-scale reactions were not carried out in sealed containers may have some bearing. No conclusive evidence was ever obtained that continuous stirring offered any advantages over thorough mixing only at the start of the reaction. Since the minimum FFA value can be made fairly consistent over a period of days, flexible plant operation would be possible. Heating of the reaction mixture is not recommended (Lorette and Brown, 1959; Radin *et al.*, 1960).

Lorette and Brown showed that MeOH present in even modest proportions promotes the early stages of the reaction, but in the case of the esterification of acids only has little influence on the ultimate conversion. In the present study, where water was initially present to liberate some MeOH from the DMP, and the total MeOH liberated would exceed that necessary for the esterification, it was expected that little or no MeOH would need to be added. The experimental investigation of this point (page 609) indicated, however, that some benefit could be expected from the addition of small amounts of MeOH, and this was done in most experiments except where methanolic HCl was employed as the acid catalyst.

The possible formation of monoglycerides through acid-catalysed interesterification of triglycerides with MeOH was examined in two of the large-scale reactions (Table V). Although some such reactions has taken place, there is

only a slight rise in the monoglyceride content, indicating that the esterification reaction (a) proceeds more rapidly than the interesterification reaction (b).

The partial replacement of DMP by MeOH cannot be considered useful, since the hydrolysis of the DMP itself produces more MeOH than is required by the reaction of esterification, and moreover the amount of DMP is then less than that necessary to scavenge the total water involved. However, lesser amounts of DMP can be employed to give any desired FFA value. With a fixed proportion of acid catalyst to oil, varying the amount of DMP gives families of parallel curves (Fig. 3).

TABLE V. Percentage monoglycerides in esterified cod oils purified by various procedures (original oil, 4.76%).

Product treatment	Experiment	
	C	D
	%	%
Micro-Cel only	6.58	6.19
Washed, settled and treated with Micro-Cel	5.66	6.24
Washed, settled and clarified	5.52	5.79
Washed, settled, clarified and treated with Micro-Cel	5.55	5.74* 5.81†

*1% Micro-Cel.
†0.5% Micro-Cel.

The esterification reaction was always associated with the formation of a black polymer which settled out on horizontal surfaces, even during agitation. This material was quite coherent and adhered sufficiently well to the surfaces to permit the esterified oil to be decanted without its being disturbed, although it could easily be removed by scrubbing. Since the amount of this material formed did not appear to be significant, it was not investigated, but the quantity appeared to be related to the proportion of acid catalyst present, suggesting that it was derived from the DMP alone (Radin *et al.*, 1960) or through a side reaction with some material present initially in the oil, or formed during the reaction, such as monoglycerides, etc. Additional amounts of this or other material precipitated out in some of the purified oils from the dimethyl sulphate reactions, but not from those where HCl was employed as a catalyst.

Although normal alkali refining procedures should be suitable as a means of purifying and stabilizing the product, the presence of the precipitate suggested that a filtration step might be advisable, and treatment with a filter aid was therefore adopted as a part of the purification procedure. As indicated in Table III, Micro-Cel appeared to be the most suitable material for this purpose, and extended treatment time at room temperature gave the best results.

The reaction mixture darkened appreciably at useful acid catalyst concentrations, the dimethyl sulphate reaction more so than the others. The purified esterified cod oil from the HCl-catalysed experiment C did not suffer from discoloration, the Gardner colours observed being: original cod oil, 15; reaction mixture treated with Micro-Cel only, 14; washed, settled and treated with Micro-Cel, 13; washed, settled and clarified, 15; and washed, settled, clarified and treated with Micro-Cel, 13. It is evident that while the product not treated with Micro-Cel is no darker than the starting material, the Micro-Cel has a powerful decolorizing effect in addition to its primary function of stabilization through removal of water, mineral acid and some of the free fatty acids. The dosages employed in these experiments, 0.5 or 1%, are modest and an exposure time of 24 or 48 hours at room temperature was employed in lieu of the industrial practice of brief treatment at elevated temperatures (Anderson, 1953b). The latter procedure could have advantages in removing traces of volatiles whose presence might render the esterified oils unsuitable for some applications. On the other hand, in many potential uses colour and traces of volatiles would be of no significance, and simple treatment would suffice, provided the product is sufficiently stable during shipping and storage. The data in Table IV indicate that stable products of low free fatty acid content can be produced by the procedures outlined above.

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Effect of Tetracycline Antibiotics on Objective and Subjective Fish Quality Tests[1]

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ABSTRACT

The effect of the antibiotics chlortetracycline and oxytetracycline on certain fish quality tests (viable bacterial count, trimethylamine nitrogen content and organoleptic rating) was evaluated. The formation of trimethylamine by the reduction of trimethylamine oxide in lingcod muscle was suppressed when chlortetracycline and oxytetracycline were used as preservatives in storage tests at 0 and 4°C. Results of the three tests on antibiotic-treated samples showed poor agreement; reasonable agreement was obtained from the tests on control samples.

INTRODUCTION

During the storage of fresh fish at refrigerated temperatures, various bacteriological and biochemical changes occur in the muscle. The methods employed to study these changes have been developed by many investigators, and a number of these methods are used to assess the quality of fish. The determination of viable bacterial counts is used in some laboratories as a measure of quality. One chemical method which is employed to ascertain the degree of spoilage of fish is the determination of the amount of trimethylamine formed by bacterial reduction of trimethylamine oxide. A common subjective test which is used as an index of quality is the organoleptic evaluation of odour development.

Investigators have shown that certain preservatives which have been used in the experimental or commercial preservation of fresh fish modify the spoilage pattern, and therefore may make the results of tests for quality invalid.

During investigations into the spoilage of cod-muscle press juice, Watson (1939) found that the reduction of trimethylamine oxide is not a function of the total bacterial population. Tarr and Bailey (1939) found from ice storage tests on dressed halibut that the incorporation of 0.1% benzoic acid in the ice suppressed the reduction of trimethylamine oxide but not bacterial increase in halibut flesh. Castell (1949) showed that less than 100 parts per million (ppm) of sodium nitrite in cod fillets retarded the production of trimethylamine and had no significant effect on bacterial development. Dyer (1949) reported that the rapid reduction of trimethylamine oxide in cod fillets is inhibited until the nitrite concentration has been reduced to about 50 ppm. From studies on two

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trimethylamine oxide-reducing bacterial cultures Castell and Greenough (1957) found that the antibiotics chlortetracycline, oxytetracycline, polycycline and nisin in concentrations from 1 to 50 ppm did not retard the bacterial reduction of trimethylamine oxide to trimethylamine by washed cell suspensions. Stewart and Castell (1960) reported that sodium benzoate inhibited the trimethylamine oxide-reducing system of resting cells of two bacterial species.

The purpose of this investigation was to ascertain the effect of the antibiotics chlortetracycline (American Cyanamid Co.) and oxytetracycline (Chas. Pfizer and Co.) on the formation of trimethylamine in lingcod muscle, and also to study the difference between viable bacterial count, trimethylamine content and organoleptic score.

MATERIALS AND METHODS

Lingcod (*Ophiodon elongatus*) were obtained from a commercial fish plant in the Vancouver area. The post-mortem age of the fish was from 2 to 3 days.

Portions of muscle approximately 1 × 2 × 2 inches (2.5 × 5 × 5 cm) were cut from fillets, and treated with the antibiotics chlortetracycline (CTC) and oxytetracycline (OTC). The muscle portions were dipped for 1 minute in a 10-ppm solution of the antibiotic, and control samples were dipped similarly in water. All samples were allowed to drain for 15 minutes after the dipping process. Subsequent to treatment, each lot of muscle was minced in a sterile meat grinder. The minced muscle was packed in polyethylene bags and then stored at 0 and 4°C for storage tests. At intervals samples were taken for viable bacterial counts, trimethylamine nitrogen determinations and organoleptic evaluations.

Viable Bacterial Counts

For the determination of the viable bacterial count, 40 g of minced muscle was added to 360 ml of sterile 3% (w/v) sodium chloride solution contained in a 1-quart (1.1-litre) wide-mouthed jar, and shaken for 3 minutes on a reciprocal shaker at 260 oscillations per minute. Appropriate dilutions were made from the shaken sample and 3% sodium chloride–Bacto nutrient agar plates were prepared. The plates were incubated at 25°C for a period of 72 hours. A Quebec colony counter was used in the determination of the number of colonies per plate.

Trimethylamine Nitrogen

The trimethylamine nitrogen content was determined by the method of Dyer (1945, 1950). A slight modification of this method was used in the extraction process; the extraction was carried out by shaking the trichloracetic acid and sample mixture on a rotary shaker at 260 oscillations per minute for 15 minutes rather than by manual shaking over a half-hour period.

Organoleptic Tests

The extent of odour development in the samples was used as an index for organoleptic evaluation. In this study, a sample was classed as acceptable when

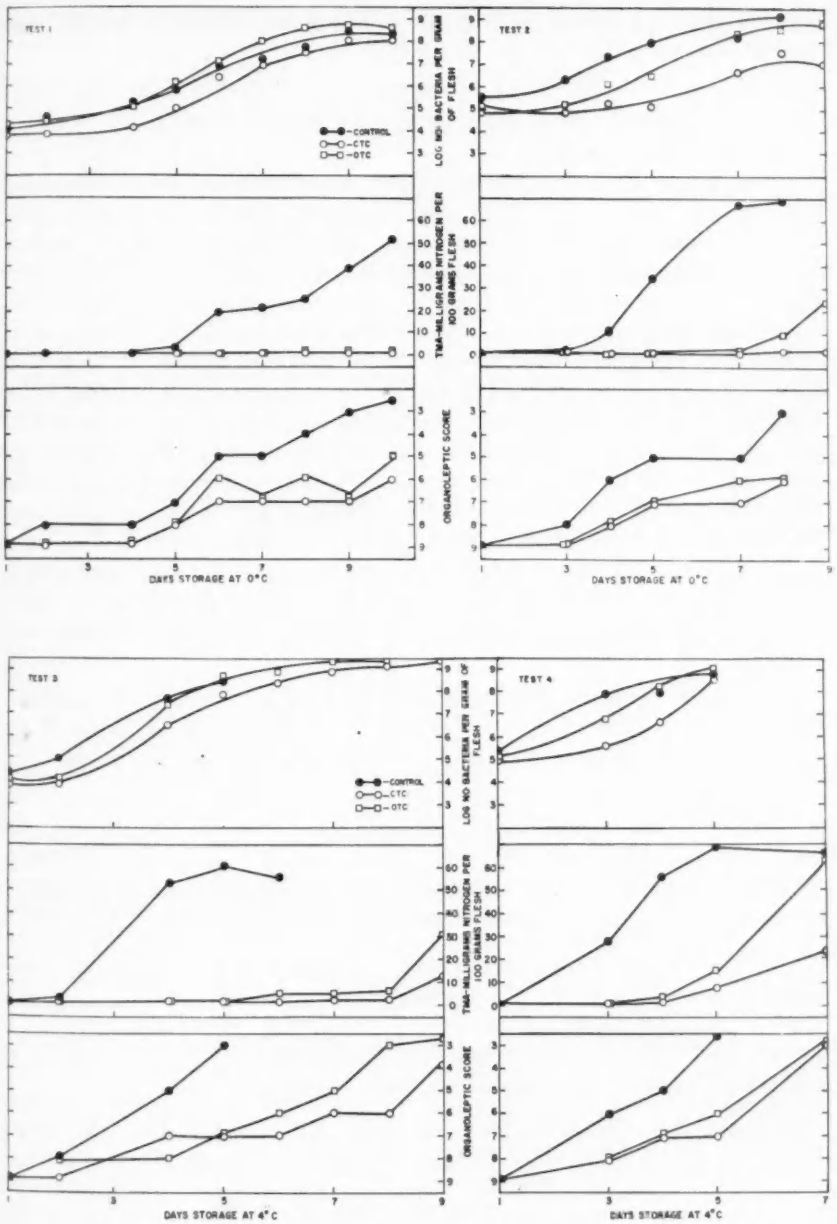

FIG. 1. Viable bacterial counts, trimethylamine nitrogen determinations and organoleptic scores on antibiotic-treated and untreated lingcod muscle.

assigned (within a scoring range of 10 to 0) a score between 10 and 5.5, and unacceptable when it scored less than 5.5.

RESULTS AND DISCUSSION

The results of four separate tests made on antibiotic-treated and untreated lingcod are presented in Fig. 1. It should be noted from the curves that chlortetracycline and oxytetracycline significantly suppress the reduction of trimethylamine oxide to trimethylamine in lingcod muscle during storage at 0 and 4°C. However, under the conditions of the tests there was not a corresponding reduction in the bacterial population. Similar results were obtained from a test in which small fillets were used rather than comminuted muscle. This lack of parallelism between trimethylamine nitrogen content and viable bacterial count of treated samples indicates that the antibiotics may inhibit the growth of micro-organisms responsible for the reduction of trimethylamine oxide, and allow the growth of non-reducing bacterial species. As reported by Castell (1949), the inhibition of certain enzyme systems by nitrite may interfere with the reduction of trimethylamine oxide without a parallel reduction in bacterial numbers. Accordingly, the antibiotics evaluated may have interfered with a trimethylamine oxide-reducing enzyme system. A reasonable degree of agreement was obtained between viable bacterial count, trimethylamine content and organoleptic score from tests on control samples.

It may be concluded from these tests that the measurement of trimethylamine content of certain species of fish may not be a suitable index for the determination of freshness when tetracycline antibiotics are used as preservatives.

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Blood pH and Mortality in Rainbow Trout *(Salmo gairdnerii)* and Sockeye Salmon *(Oncorhynchus nerka)*[1]

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ABSTRACT

Rainbow trout (*Salmo gairdnerii*) under light anaesthesia with MS 222 (tricaine methanesulphonate) died when their blood pH was lowered into the range of 6.8 to 6.9 by injection of either lactic acid or hydrochloric acid. When injection of the same quantities of either acid did not lower the blood pH into this range, fatalities did not result (one exception in 56 fish injected). The injection of much larger quantities of lactate or chloride ions in the form of sodium salts did not cause fatalities.

Very limited data for sockeye salmon (*Oncorhynchus nerka*) suggest a similar association between blood pH and mortality for this species.

INTRODUCTION

A number of studies of the effect of exercise on the pH and lactic acid content of fish blood have been made. These have been reviewed in detail by Black (1958) and Black *et al.* (1959, 1961). They have pointed out that while in some species of fish death may result from severe exercise, the primary cause of death has not been determined, although it has been suggested that two of the factors that might be concerned are (1) a decrease in blood pH and (2) an increase in lactate concentration in the blood. It appears that the tolerance of fish toward lowering of blood pH has not been established (see Hunn, 1959). The present report describes an investigation of the ability of rainbow trout (*Salmo gairdnerii*) and sockeye salmon (*Oncorhynchus nerka*) to survive a lowering of blood pH brought about by intravenous injections of dilute acids.

MATERIALS AND METHODS

Rainbow trout were supplied by the British Columbia Provincial Hatchery at Cultus Lake, B.C., and sockeye salmon fingerlings by the Biological Station of the Fisheries Research Board of Canada, Nanaimo, B.C. The sockeye were held at the Vancouver Public Aquarium and gradual acclimation to living in sea water was commenced soon after they were received. The trout were about 2 years old and the sockeye salmon about 2½ years old when the experimental work was carried out. The fish were maintained on a diet of pelleted fish food (J. R. Clark Co., Salt Lake City, Utah) supplemented once a week by ground horse heart with added riboflavin.

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When acid or salt solutions were to be injected into the fish, or when blood was to be drawn from them, they were anaesthetized by immersion in a 1 part in 12,000 solution of MS 222 (tricaine methanesulphonate, Sandoz Ltd.). The period of immersion was such that the fish were not completely anaesthetized but were quiet and easy to handle. Injections or blood withdrawals were made via the Cuvierian duct by means of a hypodermic syringe fitted with a No. 26 needle according to the method of Sano (1960) while the fish were held in air. When blood was to be withdrawn, the syringe was first rinsed with a solution of heparin (0.4 mg/ml) and then drained. The quantity of blood drawn varied between 0.3 and 0.6 ml/100 g body weight of fish. Measurement of blood pH was made with a Model G Beckman pH meter, the blood being ejected directly onto the electrodes from the syringe. Acid or salt solutions were injected at a rate of about 0.1 ml/30 seconds. Rapid injection of even a small volume of acid solution usually resulted in death of injected fish. Following the injection the fish were placed in water for 1 minute, after which blood was withdrawn from the duct on the opposite side of the fish from that into which the injection was made, then the fish were returned to water to recover from the anaesthetic. For measurement of blood lactate, blood was mixed with an equal volume of 10% (w/v) trichloroacetic acid and lactic acid was determined in the clarified supernatant solution by the method of Barker and Summerson (1941). Solutions injected were 0.135 and 0.54*M* lactic acid, 0.135*M* hydrochloric acid, 0.54*M* sodium lactate and 0.54*M* sodium chloride. All solutions were sterilized by autoclaving before use. Temperatures of the water in which the fish were held varied between 11 and 14°C during this work. Fish were exercised by chasing them in a small tank by means of a dip net.

RESULTS AND DISCUSSION

The blood pH values of a group of 12 unexercised trout (average weight 105 g, range 63 to 170 g) were between 7.05 and 7.5 with a mean of 7.3, while those of a group of 13 exercised trout (average weight 114 g, range 67 to 220 g) were between 7.1 and 7.4 with a mean of 7.25. The time required to anaesthetize the fish and measure their blood pH was about 10 to 15 minutes. Periods of exercise varied between 15 and 100 minutes but no relation between duration of exercise and blood pH was observed. Determinations of lactic acid were made on the blood of 4 fish from each group. In unexercised fish the mean value was 18 mg/100 ml blood (18 mg %) with a range of 5.5 to 28.2 mg %, while in the exercised (30 minutes) fish the mean was 36.3 mg % with a range of 15.4 to 60.4 mg %. These results are comparable to those found by various workers and summarized by Black *et al.* (1961).

Twenty-two trout (average weight 160 g, range 81 to 255 g) were injected with sodium lactate in amounts varying between 43 and 150 μM/100 g body weight, without any fatalities occurring. In 15 of these fish measurement of blood pH was made and the mean value was found to be 7.29, with a range of 7.1 to 7.5. Blood lactate in 9 fish injected with 100 to 150 μM of sodium lactate/100 g

body weight averaged 198 mg %, range 110 to 309 mg %. Six trout were injected with sodium chloride in amounts varying between 108 and 324 μM/100 g body weight without fatalities.

The results of injections of trout with lactic acid solutions and with hydrochloric acid solutions are tabulated in Tables I and II, respectively. The data indicate that under the conditions employed, a critical range in blood pH is encountered between about 6.9 and 6.8. Above this range the fish usually survived (a single fish died with a blood pH of 7.22), while below it the fish usually died (a single fish lived with a blood pH of 6.6). It should be noted that while a number of fish were injected with the same quantity of either acid, death occurred in only those in which the blood pH was lowered into or below the critical range. This indicates that death was not caused directly by the injection of

TABLE I. Survival of 2-year-old rainbow trout injected intravenously with lactic acid. (Ten additional injected fish with a blood pH of 6.4 or lower all died. There is reason to believe that in the fish with a blood pH of 7.3 and above in this and the following Tables, not all of the acid injected entered the duct.)

Weight of fish	Lactic acid injected	Blood pH after injection	Blood lactate after injection	Alive (A) or dead (D)
grams	*μM/100 g body weight*		*mg %*	
135	25	7.3	61.2	A
175	37	7.3	69	A
170	25	7.22	108	D
140	37	7.2	58.5	A
155	20	7.2	34.2	A
145	25	7.2	46.2	A
135	36	7.16	63.9	A
145	25	7.16	43.5	A
240	25	7.16	63	A
76	54	7.15	...	A
103	54	7.15	...	A
93	54	7.15	...	A
145	13	7.12	19.5	A
340	12	7.1	51.6	A
180	25	7.08	30.3	A
230	19	7.05	45	A
140	25	7.03	58.5	A
160	25	7.00	49.1	A
270	19	6.9	51.6	A
240	22	6.9	60.6	A
175	25	6.82	87	D
220	81	6.8	...	A
170	25	6.8	60.3	D
150	25	6.62	149	D
200	19	6.6	129	A
140	25	6.5	83.2	D

TABLE II. Survival of 2-year-old rainbow trout injected intravenously with hydrochloric acid.

Weight of fish	Hydrochloric acid injected	Blood pH after injection	Blood lactate after injection	Alive (A) or dead (D)
grams	*μM/100 g body weight*		*mg %*	
265	20	7.4	24.8	A
130	20	7.3	22.8	A
155	25	7.2	21	A
240	25	7.2	24.9	A
150	20	7.2	21.0	A
185	25	7.2	19.1	A
150	12	7.2	40.2	A
160	25	7.1	15.5	A
175	25	7.1	13.1	A
145	12	7.1	45.3	A
200	25	7.05	38.7	A
140	20	7.0	13.2	A
175	14	7.0	25.5	A
135	25	6.9	11.4	D
120	25	6.9	12.0	D
170	20	6.9	21.9	A
170	25	6.85	15.0	A
175	25	6.85	22.5	D
330	25	6.8	54.9	D
155	25	6.7	23.7	D

either acid by itself but by the change in pH that it brought about. It is possible that the blood of the fish which survived was in a more alkaline condition at the time of commencement of injection than was that of those that died— a possibility that is indicated by the range of pH values found in unexercised fish (*vide supra*). Fish that died did so within a few minutes, usually without recovering from the effects of the anaesthetic. Examination of the data of Tables I and II, in conjunction with those for injection of sodium lactate and chloride solutions given above, will show that death of the trout in the present work cannot be attributed to increases in either the lactate or chloride ion concentrations of the blood *per se*. However, this observation should probably not be regarded as evidence against the possibility that a high lactate concentration, if maintained for a protracted period of time, could be a contributing factor in causing death (e.g. von Buddenbrock, 1938; Secondat and Diaz, 1942; Parker and Black, 1959; Parker *et al.*, 1959).

Results of a limited study with sockeye salmon are summarized in Table III. A relation between blood pH and mortality in these fish similar to that observed in trout is indicated. Blood lactate concentrations in exercised and unexercised fish were comparable to those previously found in 2-year-old sockeye (Black, 1957).

TABLE III. Survival of 2½-year-old sockeye salmon injected intravenously with lactic acid.

Weight of fish	Compound injected	Blood pH after treatment	Blood lactate after treatment	Alive (A) or dead (D)
grams	*μM/100 g body weight*		*mg %*	
110	None—fish unexercised	7.2	46.7	A
170		7.04	25.1	A
185		7.03	25.9	A
201		7.0	178	A
180	None—fish exercised 50 min	7.04	76.5	A
165		7.3	74.5	A
200		7.3	55.8	A
110		7.25	63	A
150	Sodium lactate, 150*	7.28	154	A
145	Sodium lactate, 150	7.27	414	A
160	Lactic acid, 25	7.3	41.1	A
155		7.18	54	A
140		6.88	67.5	A
105		6.87	71.5	A
160		6.72	85.5	D
120		6.72	78.7	D
155		5.85	150	D

*This injection apparently did not all enter the duct.

The range of blood pH in which mortality began to occur in either rainbow trout or sockeye (6.9 to 6.8) is only slightly below that observed immediately after exercise or during recovery in the same species of trout (e.g. Black *et al.*, 1959). However, it should be remarked that the results in the present work may have been influenced by the experimental conditions, particularly through the use of an anaesthetic, in such a way that death occurred at a higher pH than might have been the case under other circumstances. However, this is not certain, and in our experience it would be very difficult, if not impossible, to carry out the necessary injections without the use of an anaesthetic. In this connection Leivestad *et al.* (1957) have shown that removing an unanaesthetized fish from water for 4 minutes causes a pronounced bradycardia accompanied by increased lactic acid formation in the muscles. The lactic acid subsequently passes into the blood. These workers also showed that bradycardia can be induced in fish through fear while they are submerged. It is interesting to note (Crowell and Houston, 1961) that in the dog a reduction in pH to a little below 7.0 results in a remarkable reduction in the clotting time of heparinized blood, and also that lowering the pH of blood initiates coagulation.

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rainbow trout and sockeye salmon, respectively, used in this work. We also wish to thank Dr E. C. Black, Department of Physiology, University of British Columbia, for his interest and valuable suggestions during this work, and for his critical reading of the manuscript, and Dr Murray A. Newman for the use of facilities at the Vancouver Public Aquarium.

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Skin-diving Observations of Atlantic Salmon and Brook Trout in the Miramichi River, New Brunswick[1]

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ABSTRACT

Free-living Atlantic salmon and brook trout were studied at 12 locations in the Miramichi River, New Brunswick, by swimmers wearing skin-diving equipment. Juvenile salmon were found at all locations, but were most numerous in rapids in the river headwaters. Juvenile and adult trout were common in rapids and pools of the headwaters only. Small numbers of adult salmon were seen throughout the river, mostly in pools.

The following activities of both species are described: position maintenance relative to surroundings; social, feeding, escape and investigatory behaviour.

The potential value of underwater swimming as a tool in fisheries research is briefly discussed.

INTRODUCTION

In many parts of the world underwater swimming has been rapidly increasing in popularity since the pioneer work of Cousteau, Hass and others. Books such as "The Silent World" (Cousteau, 1953) and "Manta" (Hass, 1952) as well as popular articles by many other writers have contributed to this widespread interest. Although most diving has been done for sport, as a new and exciting way to catch fish, many biologists have also gone underwater to observe and study fish and other aquatic life at first hand. Some of this work has produced results of interest to scientists and naturalists alike (e.g., Kirchshofer, 1954; Carlisle, 1961; Limbaugh, 1961).

In Canada the development of skin- and scuba-diving has been relatively slow, partly because our waters are too cold during most of the year for prolonged swimming without expensive protective clothing. Also, aquatic animals and plants are not as varied and colourful in temperate areas, such as Canada, as they are in sub-tropical and tropical regions. Thus, the conditions and incentives for free-diving are less attractive in Canada than in many other countries. In spite of these drawbacks Canadian biologists have begun to realize the value of underwater swimming as a research tool and useful results have already been produced by divers at laboratories such as the Fisheries Research Board Biological Stations at Nanaimo, B.C., and St. Andrews, N.B. (Ellis, 1962a, b; Elson, MS, 1962).

The purpose of this paper is to describe observations of fish made with the aid of simple skin-diving equipment in August 1958. The species observed were

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the Atlantic salmon (*Salmo salar L.*) and the brook trout (*Salvelinus fontinalis* (*Mitchill*)). Both of these are well-known and highly prized sport fish; the salmon is also fished commercially off Canada's east coast. Much has been written about their behaviour, but mainly from the angler's point of view, with attention generally focussed on the interaction between fish and fisherman. Some careful biological studies have been made of the behaviour of these species, either from above the surface of the water (White, 1924; Elson, 1942), through the glass walls of a tank submerged in a stream (Newman, 1956), or while the fish were held in large "artificial stream" tanks (Kalleberg, 1958; Jones, 1959). None of these methods combines freedom of movement of the observer with directness of observation so well as skin-diving does. Thus, the present observations have the advantage of less restricted viewing of the fish, while the fish themselves are free to move where they will. It was also hoped that this work would provide useful background information on which to base subsequent laboratory behaviour studies of Atlantic salmon. The results of some of these studies will be published shortly (Keenleyside and Yamamoto, 1962).

ACKNOWLEDGMENTS

Much of the stimulation for underwater swimming as an adjunct to fisheries research at the St. Andrews Biological Station has come from Dr P. F. Elson. The author has profited greatly from the enthusiastic assistance and advice given by Dr Elson during this and other diving projects.

Mr D. G. Maddison and Mr F. T. Yamamoto provided invaluable assistance in the field while this work was under way. Both were hired by the Fisheries Research Board as student assistants during the summer of 1958.

Mr R. J. Gibson kindly supplied the photographs which accompany the paper. They were taken by him in the Northwest Miramichi River in 1960 and 1961, using an underwater Robot camera. Film types are given in the figure legends.

Both Dr Elson and Mr Gibson have offered helpful comments and criticisms on the material in this paper, based on their own skin- and scuba-diving experience in salmon and trout streams. These are gratefully acknowledged, although the author takes full responsibility for the accuracy and interpretation of all observations.

METHODS

The Northwest Miramichi River and two of its tributaries in north-central New Brunswick were chosen for this study, because other research on salmon biology was in progress there at the time (see Kerswill, 1961) and field camps were located nearby. A series of twelve observation stations was selected between the headwaters and the mouth of the Northwest Miramichi (see Fig. 1). Two of these stations were on the Sevogle River, one was on Little River (both of which are tributary to the Northwest Miramichi) and all others were on the main river. Stations were deliberately chosen in sections of the river with

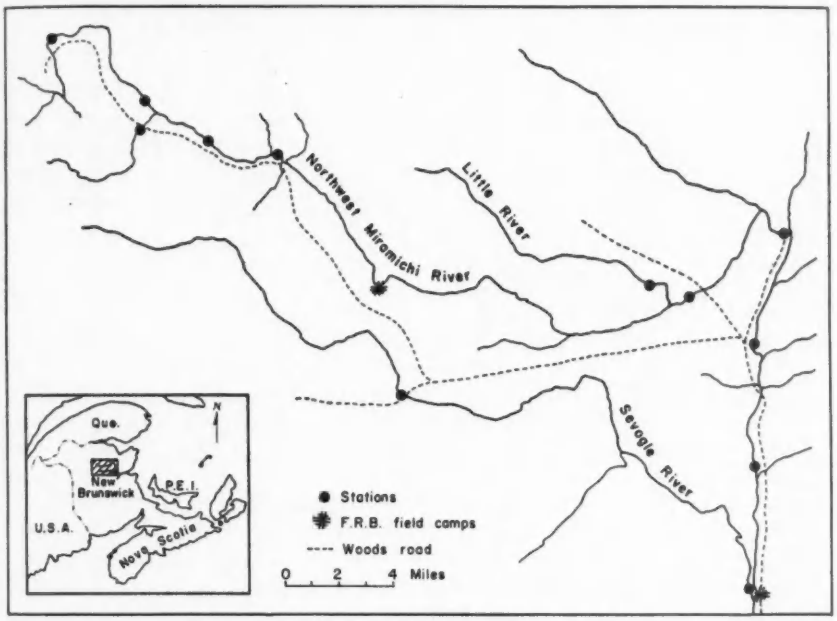

FIG. 1. Map of the Northwest Miramichi River and some of its tributaries, showing skin-diving stations. Inset map shows location of this river in New Brunswick.

different physical characteristics, so that information could be gained on the relative abundance of salmon and trout in different environments. At each station observations were made by one or more swimmers using a face mask, snorkel breathing tube and flippers. A "dry" type rubber suit was worn for protection against cold where the water temperature was below 16°C; otherwise swimming trunks were adequate. A floating viewing box was also used, with a glass bottom 18 inches square (46 × 46 cm). An adjustable mirror suspended below the box allowed the viewer to change the direction of vision below the water surface while continuing to look down through the box.

The most prolonged observations, and those which disturbed the fish least, were made by a swimmer floating at the surface and moving slowly from place to place, anchoring himself by holding onto large rocks. After observations of up to one hour the swimmer emerged and immediately made notes on the abundance of fish of different species, their location and behaviour. Records were also kept of the time of day observations were made, river depth and width, estimated speed of surface current, type of bottom, vegetation and river bank, weather conditions, water and air temperatures and light intensity at the water surface. A total of 12½ hours was spent in underwater observations over a period of 23 days.

ABUNDANCE

Only a few adult salmon and trout were seen during this study. Juvenile salmon of different sizes were seen at all stations and young trout at many of them. The number of fish at each station was apparently associated with physical features of the environment. The following statements are based on measurements of some of these features, together with rough estimates of the numbers of fish present. No attempt was made to census the fish populations accurately.

(a) Salmon Fry (Underyearlings)

These fish were more abundant over a standard area of river bottom in the upper reaches of the river than in the lower downstream sections. Thus, they were relatively more numerous where the river was narrow to moderately wide (5 to 30 m), shallow to moderately deep (15 to 50 cm), where rapids and riffles were common, where pools were small and relatively shallow (1 m maximum depth), and where the water was cool (10.0 to 17.0°C). They were less common further downstream where the river was broader (50 to 100 m) and deeper (30 to 100 cm), where rapids were scarce, pools were longer and deeper (2 m maximum depth) and the water was warmer (15.0 to 21.0°C). Fry were most commonly found in rapids where the bottom was made up of small gravel and stones; occasionally they were found over sandy bars. Fry swimming in water less than 15 cm deep may have been missed by the observer, due to the difficulty of seeing through a face mask in very shallow water.

(b) Salmon Parr (from 1 to 4 Years Old in This River)

Parr were most common in the same sections of the river where fry were most abundant, except that parr generally stayed in deeper, faster water and over bottom that varied in size from small gravel to cobble rock, with occasional large boulders. Silt-free bottom was characteristic of both salmon fry and parr habitat.

(c) Adult Salmon

Most adults encountered were in deep, quiet pools, where they rested quietly close to the bottom. A few were seen in narrow, fast-flowing channels. Only a small number of adult salmon was seen, and no further generalizations can be made about their abundance in different parts of the river.

(d) Trout (Juveniles and Older Fish)

Trout were seen only at the upriver stations, in the areas of greatest density of salmon fry and parr. Trout fry were usually seen in shallow, slow-moving water along the river's edge; older fish were found in deeper water, where the river was relatively narrow, rough and turbulent, or where deep channels flowed swiftly under banks overhung with alders. Occasionally trout of various sizes were seen in and near pools. The river bottom in areas where trout were most common varied from clean gravel and cobble rock in turbulent water to sandy bars in the vicinity of deeper pools.

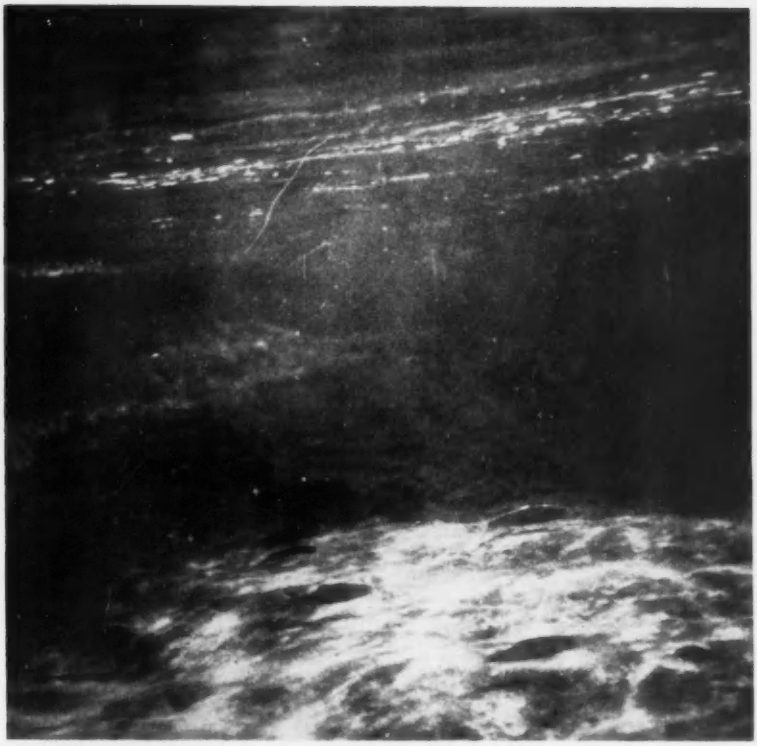

FIG. 2. Five salmon parr holding position over conglomerate rock in the Sevogle River. Photograph taken in the summer of 1960, using Kodak Safety Plus X Pan film. This and all subsequent photographs taken by R. J. Gibson while skin-diving.

FIG. 3. Adult salmon swimming upstream immediately after leaving counting fence trap, Northwest Miramichi River. Photograph taken on Kodak High Speed Ektachrome colour film, July 13, 1961.

FIG. 4. Adult salmon and grilse holding position near the downstream end of a large pool, Northwest Miramichi River. Photographed on Kodak Plus X Pan film, September 26, 1960.

FIG. 5. Grilse in a pool, Sevogle River. Photographed on Kodak Tri X Pan film, July 4, 1961.

All of the above generalizations are based on observations made during daylight hours; no nocturnal observations were attempted. At night young Atlantic salmon apparently move inshore to quiet, shallow water and settle to the bottom (Elson, 1942). Adult salmon generally move upstream from pool to pool during periods of low light intensity (personal observations at research counting fences on the Northwest Miramichi River).

MAINTENANCE OF POSITION

(a) Salmon

Although most young salmon live in fast flowing, often turbulent water, they are almost stationary much of the time, holding position on or near the bottom while facing into the current. Position is maintained either by direct contact with the substrate or by constant swimming. Occasionally a fish will dart a short distance away to pick up food or to attack or chase an approaching fish, but usually it quickly returns to its previous position.

Some young salmon were seen resting with the ventral body surface in contact with the substrate, in which case they appeared able to maintain position with little effort, even in fast water. Others stayed close to the bottom with only the pectorals, pelvics and occasionally the anal fin touching the substrate. Contact between substrate and the large pectoral fins appears to help anchor the fish in position, as the water flows against the widely spread fins and forces them down against the bottom. Some larger parr were seen holding position up off the bottom for long periods by swimming actively against the current. This occurred generally near pools, where the water flowed more smoothly than in the rapids. Figure 2 shows salmon parr holding position near the bottom by swimming actively against the current.

Young salmon that are in contact with the bottom often rest with the head higher than the tail. This position is maintained by the relatively large pectoral fins, which support the head and fore part of the body. A fish holding position over fine gravel often rests with the front part of the body on the downstream, downward sloping part of a small stone, and with the hind end of the body trailing down behind the stone. As pointed out by Kalleberg (1958) and confirmed in this study the degree of contact between fish and substrate depends largely on the speed of water current. Young salmon in relatively slow-moving water were often seen resting lightly on the bottom with only the tips of the pectoral fins and the ventral lobe of the caudal fin in contact with the gravel, and the head held well off the bottom. In faster water the fish were more often seen with the entire ventral body surface pressed against the substrate. The typical head-up posture of the young salmon may be related both to the capture of prey and defence against predators; with the head held up the fish may be able to see further through the water and thus respond more quickly to prey or enemies.

In many places, especially in very fast water, young salmon were found resting on sand or fine gravel directly behind large stones. There they oriented in any direction, including downriver, the direction of orientation probably depending on the system of water currents flowing around the large stone.

Occasionally young salmon were found in what appeared to be highly unlikely places for small fish, for example, "clinging" to the rocky sides of a deep channel where the water current was fast and turbulent, or almost buried under gravel in the middle of extremely fast-flowing rapids. The fish no doubt maintained these positions by taking advantage of the patterns of water movement around or against the rocks, or by sheltering from the direct force of the current by burrowing under small stones.

Adult salmon seen during this study were usually found near the bottom of pools. They were seen most commonly at the upper and lower ends and in the deepest, quietest parts of pools. Most of the time they swam against the current just fast enough to maintain position; they were not found resting in contact with the substrate. (P. F. Elson and R. J. Gibson in a personal communication report that they have on occasion seen adult salmon resting directly on the bottom in rivers, especially in areas of quiet, slow-moving water.) Often these large fish held position near boulders, bridge foundations and other large objects in the water. Sometimes one of them left its resting position and swam vigorously around the pool, occasionally jumping clear of the water. No attempt was made to correlate jumping activity with physical features of the environment. A few adult salmon were seen in narrow channels swimming vigorously to maintain their position for long periods against the fast current. Photographs of grilse (salmon that have been to sea for 1 year) and older adult salmon are shown in Fig. 3, 4 and 5.

(b) Trout

Young trout do not maintain as close contact with the substrate as do young salmon, but usually hold position in a stream by swimming actively against the current. Thus, trout often appear more active than young salmon because they swim freely in the water and, in places where the current is turbulent, are moved around constantly as they try to maintain position.

Occasionally a large trout was found alone in a channel beneath a river bank, usually in places overhung with alders. These larger fish also maintained position by swimming against the current rather than by contact with the substrate.

SOCIAL BEHAVIOUR

(a) Salmon

Juvenile salmon in fresh water are territorial, i.e., each fish maintains a position relative to the substrate and defends an area around this position by chasing away other fish that enter the area. Thus, young salmon in a river are generally scattered, some fish feeding, some threatening or chasing others away from their territories and some resting quietly near the bottom. This contrasts with schooling fish, where typically all members of a school perform the same activity (feeding, swimming, resting) together and all fish remain close to each other. Territorial behaviour in young Atlantic salmon has recently been described on the basis of aquarium observations (Kalleberg, 1958; Keenleyside and Yamamoto, 1962).

During the present study it was difficult to determine accurately the limits of the territories of the young salmon. The boundaries probably depend on the size of the resident fish, the density of the fish population and the topography of the surroundings. Territories tend to be larger where the resident fish are large, where the population is sparse or where the bottom topography is relatively smooth and even. Similar conclusions were drawn by Elson (1942) and Kalleberg (1958).

Although it is difficult when swimming to study in detail the conflicts that occur between territory-defending fish, some features of this behaviour were clearly seen. When a young salmon swims into the territory of another the latter rises from its resting position on the bottom and approaches the intruder. Usually the intruding fish retreats quickly and the resident settles back into its former resting place. If the intruder is slow to retreat, or if it threatens the resident, a fight may result between the two fish. The fight can take the form of mutual threatening, nipping, or biting and usually ends with the intruder fleeing from the territory.

In general, aggressive behaviour was not common among these salmon living under natural conditions. At stations where fish were most abundant territory defence was occasionally seen as one fish trespassed onto another's territory, usually in the pursuit of food. On some occasions a fish frightened away from its resting position by approach of the observer would stimulate attack by other fish as it swam through their territories.

No signs of aggressive territorial behaviour were seen among adult salmon during these observations. When several adult fish were in the same pool they appeared to behave as a school, i.e., all swam about actively together, or all maintained position close to each other, with no signs of mutual aggressiveness. During spawning in October and November the Atlantic salmon, in common with other salmonid fish, defend territories around the nests in which they lay their eggs. No signs of this aggressiveness were seen during the present study, which was made in August.

(b) Trout

Young trout were observed to show more than one kind of social behaviour, in contrast to young salmon which were almost exclusively territorial. In shallow rapids where the bottom was gravel or cobble rock, young trout behaved very much like young salmon, each fish maintaining a territory for long periods by chasing away all intruders. The degree of aggressiveness shown by the resident trout varied, depending probably on the behaviour of the intruding fish. Usually swimming towards the intruder was enough to induce it to retreat quickly. If the intruder was slow to retreat, or if it threatened the resident, the latter would actively attack and chase it, sometimes nipping or biting at its tail. Sometimes these more vigorous fights lasted until the resident fish was far from its original position. Almost invariably it quickly returned to its territory when the fighting had stopped.

Trout were also found congregated in large numbers in pools and quiet, weedy backwaters partially separated from the main river by sand or gravel

bars. It was not uncommon to find 60 to 75 young trout grouped closely together and holding position over such a bar, facing into the current that spilled over into the pool from the main river. These trout resembled typical schooling fish.

Only a few large trout were seen during this work and they were found alone in channels and pools where they may have been defending territories, although no defensive behaviour was seen. Large trout were not seen in groups or schools.

FEEDING BEHAVIOUR

(a) Salmon

In general, young salmon feed actively during the daytime, when the present observations were made. They feed both on bottom organisms (mainly aquatic insect larvae) and on particles floating in the water. The latter may be insect larvae dislodged from the bottom, insects rising to the surface to emerge, or terrestrial insects that have fallen into the water. In all cases, the feeding reaction of young salmon is relatively stereotyped. The fish resting on or near the bottom in its territory turns slightly to face towards the prey object, then swims directly towards it, snaps it up and quickly returns to its original position. Sometimes the organism is then spat out of the mouth and taken in again several times until it breaks into pieces which are swallowed, or until it drifts away with the current.

Young salmon holding position well off the river bottom, such as some larger parr around the edges of deep pools, feed mainly on floating organisms. These fish were not seen to settle and pick prey off the bottom.

Adult salmon observed during this period did not feed. It is well known that sexually maturing Atlantic salmon generally cease feeding even before entering fresh water from the sea (Jones, 1959).

(b) Trout

The younger trout appeared to feed on the same two types of food that young salmon did, but concentrated mainly on floating organisms. Only occasionally did they take food off the bottom. This difference in observed feeding habits of the two species may be related to the fact that most trout held position off the bottom, where floating particles would be encountered more frequently and could be captured more easily than if the fish were resting on the bottom. Most young salmon, on the other hand, were either in contact with or very close to the substrate.

No observations were made of adult trout feeding.

ESCAPE AND INVESTIGATORY BEHAVIOUR

(a) Salmon

Young salmon were not easily frightened away by a swimmer wearing skin-diving equipment, as long as he made no sudden violent movements. Most young salmon could be approached to within 20 or 25 cm without causing evident alarm. When frightened they darted quickly away and did not return to their

original position until the swimmer left the area. Fish in contact with the substrate were easier to approach than those holding position off the bottom. Some fry settled down among the stones when approached by a swimmer and could only be induced to leave such hiding places by prodding with a stick or fingers.

Occasionally salmon parr showed a type of investigatory behaviour that can best be described as "curiosity". Such fish would approach the swimmer and often follow him for some distance, showing no signs of aggressiveness. On one occasion lasting about 10 minutes a group of 10 or 12 parr gathered closely around the author who lay motionless on the river bottom. These fish did not leave until clearly frightened by vigorous and repeated movements by the swimmer. Similar behaviour of young Pacific salmon was noted by Ellis (1962a).

By approaching slowly and carefully it was sometimes possible to swim to within 2 metres of adult salmon resting in pools. These fish did not appear alarmed until the swimmer was almost within reaching distance. Then they dashed quickly away and did not return to the same place until the swimmer had left the pool. Mr R. J. Gibson (personal communication) reports that grilse in shallow, headwater pools are difficult to approach underwater, and attributes this to increased wariness of the fish due to relative lack of cover in such places. Ellis (1962a) found it much easier to swim close to adult Pacific salmon when they were crowded in small pools and were facing strong currents than when they were swimming in large pools or lakes. Atlantic salmon parr have been observed to exhibit similar behaviour in small swift pools as compared with large quieter pools (Elson, personal communication).

(b) Trout

Young trout were less easily alarmed and more "curious" than young salmon. Usually a swimmer could move to within a few centimetres of the trout, some of which occasionally nibbled at his fingers, arms and legs. They were only frightened away by vigorous movements by the swimmer. Older trout were more easily disturbed and usually retreated quickly when the swimmer was 2 or 3 m away.

CONCLUSIONS

Many of the aspects of salmon and trout behaviour described in this paper will be familiar to sport fishermen and biologists who have carefully observed these fish from river banks and other vantage points. Some of the behaviour, such as aggressiveness associated with territory defence, has been described in greater detail than here, from studies of fish in aquaria (Kalleberg, 1958; Keenleyside and Yamamoto, 1962). However, observations from above water are restricted by surface disturbances, especially in rapids where juvenile salmon tend to be most plentiful, and also by the extreme caution required to avoid alarming the fish. Aquarium experiments may suffer from the confined space and unnatural surroundings of the laboratory. Underwater observing of fish in the field has drawbacks also, such as dependence on relatively clear water condi-

tions, so that the fish can be seen. But when conditions are suitable, underwater swimming can provide the biologist with unequalled opportunities to study undisturbed fish in their natural surroundings.

This investigation suggests two ways in which skin-diving can be of direct benefit to fisheries biologists. First, information on the density of fish populations obtained by traditional census methods (electrofishing, seining, angling) can be checked. This should be easier with species such as Atlantic salmon, where the juvenile fish appear to remain in the same locality for long periods; schooling fish often swim rapidly over wide areas and will thus be more difficult for swimmers to count. Also, the precise distribution of the fish within their habitats can be determined more accurately by direct observation than by traditional methods. Second, the biologist can gain first-hand knowledge of the fish's behaviour by swimming near them carefully and patiently. In this way his field observation techniques can begin to approach in accuracy and value those of the ornithologist and mammalogist. With the still greater versatility provided by scuba-diving gear (using compressed air rather than breathing through a snorkel tube) underwater swimming may soon become one of the most valuable field tools available to the fisheries biologist.

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Physical Properties and Hydrostatic Function of the Swimbladder of Herring (*Clupea harengus* L.)[1,2]

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ABSTRACT

Living herring at the depth of adjustment had a mean sinking factor of 1003, density of 1.026 g/ml, relative sensitivity of 0.8 and percentage swimbladder volume of 4.2. Neutral buoyancy was attained at a mean pressure reduction of 5.5% from the adjusted pressure. Swimbladder gas was under an average excess pressure of 1 cm Hg. Gas was released through the posterior swimbladder duct during pressure reduction in 105 out of 109 herring observed. Gas release occurred at a mean pressure decrease of 6% in rapidly swimming herring, at 32% in moderately swimming fish and brought the herring to within 19% of perfect adjustment to a new reduced pressure within half an hour. Herring could compensate for their increased buoyancy during pressure decrease until this was reduced by gas release. Decompression at rates up to 123 cm Hg/sec was not fatal after 16 hours at the greater pressure. No recovery of buoyancy after gas loss occurred in herring held 24 hours in running sea water even if fine air bubbles were present. Recovery occurred if these fish had access to the surface. Gas production by bacterial activity as a means of restoring buoyancy was not established. Herring responded to rapid pressure increases by swimming upwards. They could compensate for their increased density following pressure increase of 300% and survive increases of 430%. Herring from 10 to 25 feet depth at sea were positively buoyant at surface pressure when anaesthetized. Thus in nature herring are adjusted to pressures greater than surface pressure. It is suggested that they take in air when feeding at the surface at night and slowly pass this to the swimbladder on returning to greater depths by day.

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INTRODUCTION

IN SEVERAL RESPECTS the anatomy of the herring swimbladder is unusual among physostomes suggesting that it might deviate from the normal in function as well. Its anatomy has been described in detail by several authors including Beaufort (1909), Bennett (1880), Magnan (1929), Maier and Scheuring (1923), and Ridewood (1891). Typically in physostomes the pneumatic duct passes between the oesophagus and the swimbladder but in the herring the pneumatic duct leaves the hind end of a long caecum which forms the greater part of the stomach (Fig. 1). As this caecum lies in a dorsal position close to the swimbladder and extends for most of the length of the body cavity any gas in contained would contribute to the buoyancy of the fish without upsetting its equilibrium. Maier and Scheuring (1923) showed that the pneumatic duct has a projection from its inner wall forming a spiral valve. This may restrict the movement of gases to an inward direction only and allow an excess pressure to be maintained inside the swimbladder.

The herring swimbladder is also unusual, but not unique, in having a posterior duct which passes directly to the exterior to open beside the anal and urinogenital apertures. A common sphincter surrounds these openings (Maier and Scheuring, 1923). In a related species (*Clupea sprattus*) gas liberation through this posterior duct was seen by Verheijen (1953), who later (1956) observed this in herring but gives no details. In the present investigation the physical properties and functions of the swimbladder in intact, living herring were studied.

MATERIAL

Herring 11 to 20 cm long were obtained from weirs in Passamaquoddy Bay, N.B. All transfers of fish from one container to another were made without removing the fish from water. Herring used in laboratory studies were held in

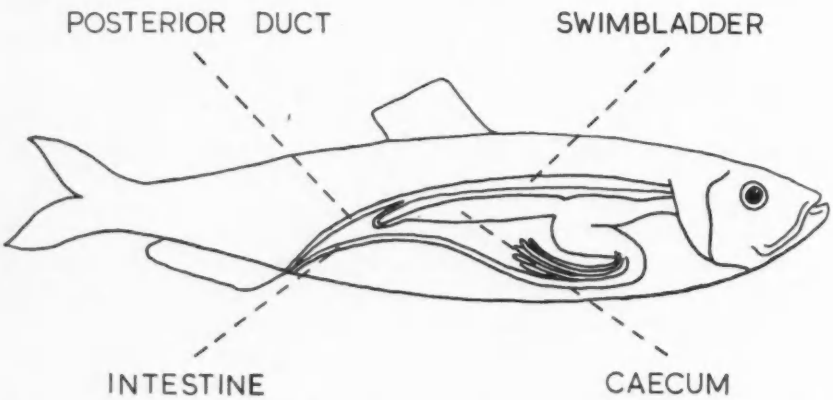

FIG. 1. Diagram of the swimbladder and its connections in herring. The pneumatic duct passes between the posterior end of the caecum and the swimbladder.

captivity until required and it was assumed, because herring held 3 and 14 days gave the same values on testing, that 3 days were adequate for adjustment to the pressures in the holding tank. For convenience it was assumed that the herring had adjusted to the hydrostatic pressure at the bottom of the tank, a total pressure of 76 + 2.6 cm Hg, as by day, at least, the herring swam close to the bottom.

A. THE HERRING ADJUSTED TO CONSTANT DEPTH

A1. Introduction

The efficiency of the swimbladder as a hydrostatic organ can conveniently be expressed by calculating the sinking factor, an expression introduced by Lowndes (1942) for 1000 times the ratio of the density of a fish to the density of its environment. Direct determination of the density of herring by weight and volume measurements is not feasible as herring release gas too readily from the swimbladder. For this reason the method given by Alexander (1959a and b), which enables the physical properties of the swimbladder of intact, lightly anaesthetized physostomes to be determined, was used in this investigation. By this method the volume of swimbladder gas is calculated from its recorded volume change with pressure.

A2. Physical Properties of the Swimbladder

Apparatus. A slightly modified form of Alexander's (1959a) apparatus was used (Fig. 2). The herring were tested individually in a 6-litre Pyrex flask having the same depth (36 cm) as the holding tank. Volume changes of the intact fish with changes in applied pressure were shown as movements of a water meniscus along a capillary tube of 0.0505 ml/cm bore.

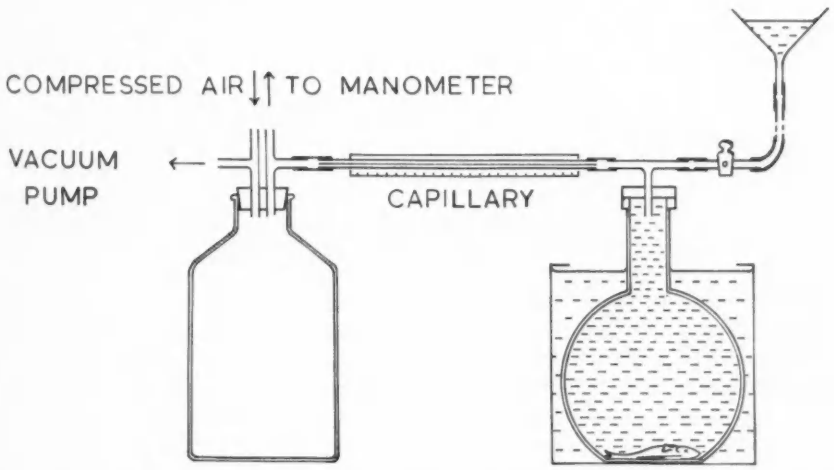

Fig. 2. Apparatus used to determine the physical properties of the swimbladder in living herring

METHOD. Sea water in the flask, water bath and the boiled sea water used in the experiment were initially at the same temperature as the stock tank. The flask was immersed in the stock tank until one herring swam into it, when it was placed in the water bath and 1 litre of boiled sea water and 0.24 g of MS222 (Sandoz Ltd., Basle) added. The boiled sea water was shown in a test run to reduce the gaseous content of the water in the flask sufficiently to prevent gas coming out of solution at the lowest pressure. The herring, lightly anaesthetized by MS222, sank to the bottom of the flask. The flask was attached to the rest of the apparatus in such a way that all air bubbles between the fish and the meniscus were excluded. As the results could be upset by fish liberating gas during this procedure the herring were kept under continuous observation and any liberating gas were rejected.

When the herring ceased to move the position of the meniscus was noted successively at positive manometer pressures of 0, 2, 4, 6, 12, 18, 24, 0 cm Hg. These values after correction for distortion of the apparatus, determined in a blank run, and for volume changes due to temperature or gas solubility shown by the difference in the two values at 0 cm Hg, gave the change in volume with pressure of the gas in the swimbladder of the fish.

The pressure was then reduced to manometer −36 cm Hg, causing the herring to release some gas from the swimbladder. The experiment was then repeated to give the volume change with pressure of the same mass of gas now partly in the swimbladder and partly in the neck of the flask. After return to 0 cm Hg the pressure was reduced to −40 cm Hg on the manometer causing further gas release and the series of pressure changes were repeated. It was found after corrections for distortion and temperature that the results following reduction to −36 cm Hg and −40 cm Hg agreed so that in both instances the gas was not constrained by the swimbladder wall and a mean value for the determination could be used in further calculations. Such a gas, being unconstrained, would obey Boyle's law and from its change in volume with pressure the total volume at manometer zero can be determined.

After each run the fish was blotted dry, weighed and discarded.

(1) SWIMBLADDER VOLUME. The swimbladder volume at the pressure at which the fish was adjusted can be determined from the results by a method given by Alexander (1959a), which for herring may be stated as follows. It was found in the herring that the volume change from 12 to 18 cm Hg for the unconstrained gas and for the gas when still contained entirely within the swimbladder was the same within 0.2 ml for all 16 fish tested. Thus, at 12 and 18 cm Hg the gas in the swimbladder is not compressed by the swimbladder wall and its volume equals that of the unconstrained gas. This allows the observed volume changes with pressure for both parts of the experiment to be plotted on the same graph with a common origin at 18 cm Hg (Fig. 3). From the volume change with pressure, calculated from the meniscus movement over the range 0 to 18 cm Hg multiplied by the capacity of the capillary bore, the total volume of the unconstrained gas at manometer zero was determined. The volume of this gas when contained in the swimbladder was less than its unconstrained volume

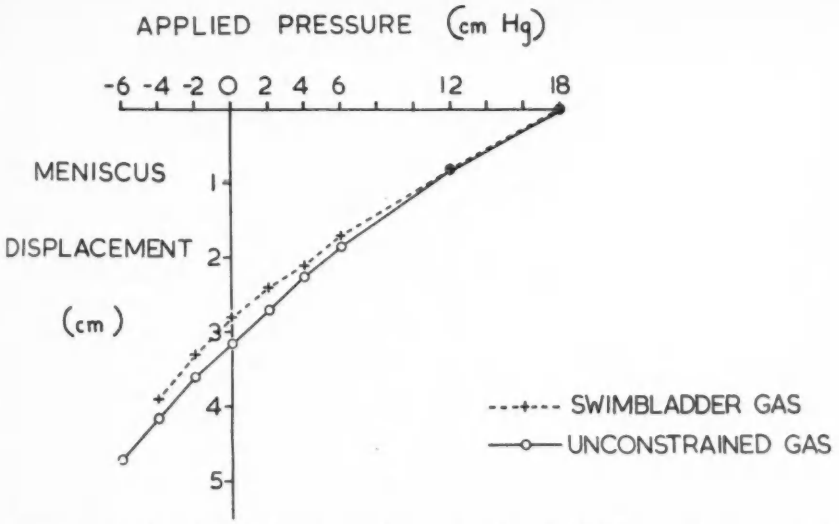

FIG. 3. Graph of meniscus displacement against pressure for swimbladder gas and unconstrained gas for fish C in experiment A2.

by an amount represented on the graph by the difference in meniscus position for the unconstrained and swimbladder gas at manometer zero.

Swimbladder volume expressed as a percentage of the mass of the fish (following Alexander's method) was found to have a mean value of 4.1% (Table I). Expressed on a volume to volume basis by making use of the density of the fish which is determined later (Section A4), the true percentage volume of the swimbladder has a mean value of 4.2%.

(2) EXCESS PRESSURE. As the volume of gas in the swimbladder is less than its volume when unconstrained the swimbladder walls must be compressing the gas at manometer zero. The pressure exerted by the walls on the gas can be read directly from the graph of results for each fish (Fig. 3) as it equals the pressure at which the unconstrained gas has the same volume as the swimbladder gas at manometer zero. The mean excess pressure was 1.1 cm Hg (Table I).

(3) RELATIVE SENSITIVITY. Alexander uses the term relative sensitivity for the ratio of the volume increase of swimbladder gas to unconstrained gas over the range 0 to 2 cm Hg multiplied by the ratio of unconstrained to swimbladder gas volumes at manometer zero. The mean value for herring was 0.8 (Table I).

A3. PRESSURE REDUCTION CAUSING NEUTRAL BUOYANCY

APPARATUS AND METHOD. A 6-litre flask attached to a pressure reservoir and manometer was used to determine the pressure reduction from the depth of adjustment which would cause lightly anaesthetized herring to rise from the bottom of the flask. The 23 herring tested had been held for 3 to 14 days in a stock tank and were assumed to have adjusted to a total pressure of 78.7 cm Hg, the same pressure as at the bottom of the flask.

TABLE I. Physical properties of the swimbladder of herring.

Fish	Period for adjustment	Mass	Excess internal pressure	Relative sensitivity over 0 to +2 cm Hg	Vol. swimbladder ÷ Mass of fish
	days	*g*	*cm Hg*		*%*
A	3	10.35	1.1	0.89	5.33
C	5	20.30	1.6	0.91	4.12
D	6	12.18	1.6	0.51	3.28
E	7	15.76	1.8	0.46	3.23
F	7	14.52	2.0	0.88	3.90
G	3	24.88	1.4	1.02	4.38
H	6	9.08	1.2	0.0	4.25
I	6	9.84	1.4	0.68	4.59
J	6	9.78	0.5	0.81	3.72
K	6	14.40	1.8	0.59	3.85
L	6	20.18	2.0	0.82	4.59
M	7	9.88	0.4	1.21	4.27
N	7	9.89	0.0	1.00	4.43
O	7	25.42	0.6	0.87	4.26
P	7	11.30	0.4	0.58	3.00
Q	7	17.08	0.4	1.01	3.97
Mean		14.68	1.1	0.77	4.07

RESULTS. The mean pressure change from manometer zero or flotation pressure for the 23 herring tested was found to be −4.3 cm Hg (standard deviation, $s = 1.5$) at a mean temperature of 10.4°C and atmospheric pressure of 76.1 cm Hg. As the herring were assumed to have adjusted to a total pressure of 78.7 cm Hg, neutral buoyancy was obtained at an average pressure reduction of 5.5% from the adjusted pressure.

A4. SINKING FACTOR AND DENSITY CALCULATED FROM A2 AND A3.

Calculation of the sinking factor of herring from the data given in Table 1 using Alexander's (1959a, b) method gives a value of 1001.8. However, this method involves certain assumptions which, for the herring, may not be justified. It assumes that the density (g/ml) of the fish is approximately equal to unity so that mass instead of volume may be used in calculating percentage volume of the swimbladder. It also assumes that relative sensitivity determined over the range of manometer zero to +2 cm Hg is equal to the ratio of change in volume with pressure for the swimbladder gas against the unconstrained gas over the range of −4.3 (the mean flotation pressure) and manometer zero. Data on volume change with pressure below manometer zero are available only for fish A, C and D, but these data do not support such an assumption. While these 3 fish showed a mean relative sensitivity of 0.77 between 0 and +2 cm Hg, identical with the mean for the whole group, yet their mean relative sensitivity over the range −4 to 0 cm Hg was 1.11. Substituting this value alone in Alexander's formula raises the calculated sinking factor from 1001.8 to 1002.6.

To overcome these difficulties, a different method of calculation was used which only requires the assumption that the density of herring may be determined by combining data from the two herring groups used in A2 and A3. It was found in Section A3 that the mean flotation pressure was −4.3 cm Hg in sea water of density 1.0230 g/ml. At this pressure the fish have neutral buoyancy so that their density equals that of the sea water. Hence as their mean mass is 14.6775 g their mean volume at neutral buoyancy must be 14.3473 ml. At manometer zero, the pressure to which the herring are adjusted, their mean mass remains the same but the mean volume decreases to $14.3473 - V \times 4.3 \times 14.3473$ where V is the decrease in volume in millilitres per millilitre of total volume at neutral buoyancy/cm Hg increase in pressure. The mean value of V based on fish A, C and D of Section A2 was 7.496×10^{-4}. From mean mass and mean volume at the pressure of adjustment the density of herring was calculated directly and was found to be 1.026 g/ml.

From its density the sinking factor of herring can be calculated as follows:

$$\text{Sinking factor} = \frac{\text{Density of fish}}{\text{Density of environment}} \times 1000$$

$$= \frac{1.026}{1.023} \times 1000$$

$$= 1002.9$$

A5. Discussion

The swimbladder as a hydrostatic organ. Herring living with access to the surface were able to adjust their density, through changes in swimbladder volume, so that their sinking factor of 1003 closely approached the value of 1000 which would occur if the herring had neutral buoyancy. Thus functionally, at least in herring living close to the surface, the swimbladder acts as a hydrostatic organ and enables the herring to maintain its position at the depth of adjustment with very little expenditure of energy used to counteract the pull of gravity. The herring is able to achieve this close adjustment to its environment with a lower percentage volume of swimbladder gas (4%) than the mean of 5% based on the 7 marine fish with well-developed swimbladders and sinking factors below 1008 listed by Jones and Marshall (1953). Alexander (1959b) has shown that the amount of energy expended to keep a fish at a new depth is approximately proportional to the product of percentage volume and relative sensitivity for small movements up or down from the adjusted pressure. The relative sensitivities for the marine fish listed by Jones and Marshall are not known but if they are of the same order as in the herring the product of percentage volume and relative sensitivity would be greater in these fish than in the herring. Under such circumstances the herring would have an advantage over these other marine fish in having a lower change in buoyancy with pressure and hence could make greater excursions about the depth of adjustment for the same expenditure of energy in compensatory movements.

Previous determinations of density and sinking factor. Magnan (1929) obtained a value of 1.061 g/ml for the density of herring which Jones and

Marshall (1953) describe as being surprisingly high for a fish with a well-developed swimbladder. Such a density would give the herring a sinking factor of 1034. It is understandable that such a high value for density should be obtained unless great care were taken, as herring readily lose gas from the swimbladder. Even fish which die under anaesthesia will release gas without further handling.

As the percentage volume of the swimbladder and the density of the whole herring have been determined here it is possible to calculate the density of herring without the swimbladder. The calculated density of the rest of the fish is 1.071 g/ml, a result which when compared with that of Magnan suggests that most of the gas had been lost from the swimbladders of the herring he tested.

B. THE HERRING SUBJECTED TO PRESSURE DECREASE

B1. Introduction

The decrease in pressure as herring rise in the water, as in all fish with an extensible swimbladder, will cause an increase in the volume of the swimbladder gas. Unless this gas can be removed in some manner from the swimbladder a limit is placed on the extent of these upward excursions either because the swimbladder would rupture or because the increased buoyancy would carry the fish helplessly to the surface. In the herring gas could leave the swimbladder directly through the posterior duct or indirectly through the pneumatic duct, stomach and mouth or anus.

B2. Mechanism of Gas Loss

Observational material. During the present investigation the liberation of gas from 109 unanaesthetized herring in water whose gaseous content was below saturation was observed. These observations were made during any experiments where these conditions were satisfied, ensuring that the observed gas came from the fish and not out of solution, and so are not uniform throughout the series.

Results. In only 1 fish of the 109 observed was gas seen to pass to the exterior through both mouth and posterior duct. In 104 herring the gas was expelled intermittently in a stream of small bubbles from the posterior duct. These bubbles usually appeared while the fish were swimming and were not accompanied by any change in behaviour. The possibility that this gas had followed a devious path through the pneumatic duct, stomach, intestine and finally been liberated through the anus into the common opening with the posterior duct was discounted as no faecal matter was ever seen to leave the fish with the flow of gas. In 4 of the observed fish gas was released through the mouth or gill arches during well-marked spitting movements. It is possible that the gas in these instances was from the stomach and had never been in the swimbladder. From these observations it appears that the normal mechanism of gas loss in the herring is by direct release to the exterior through the posterior swimbladder duct.

B3. Pressure Reduction causing Release of Gas

Material. Of the herring tested at a pressure reduction of 0.1 cm Hg/sec the 20 fish of group A1 and 5 fish of group A2 had been given 42 days to adjust to a total pressure of 79.5 cm Hg and the 20 fish of group B 3 days to adjust to 78.6 cm Hg. The 6 fish of group C were tested at higher rates of pressure reduction from their adjusted pressure of 79.7 cm Hg.

Apparatus. The herring were tested in a 6-litre flask attached to a pressure reservoir and manometer. A loose plug of netting in the neck of the flask kept the test fish in the body of the flask and a wet cloth draped partly round the outside was found to reduce its rate of swimming.

Method. The flask was immersed in the stock tank until one fish swam into it. The flask was then attached to the rest of the apparatus and the fish observed until it was swimming at a normal rate. The pressure was then reduced and the manometer reading at which gas was first liberated was noted.

Results. The pressure reduction causing gas release was expressed as a percentage decrease of the total pressure to which the herring had adjusted. In this form the results from group A1 and B which both relate to moderately swimming fish undergoing pressure reduction of 0.1 cm Hg/sec could be compared and as there was no significant difference between their means ($t = 0.42$; d.f. = 38) the results were combined. The mean percentage pressure reduction for the 40 fish in groups A1 and B was 32.0% ($s = 9.8$). In contrast the 5 fish of group A2, which are treated separately because they swam extremely rapidly while being tested, gave a mean value of pressure decrease of 6.4% ($s = 2.6$) which was significantly different at the 0.1% probability level from the mean based on normally swimming fish ($t = 5.7$; d.f. = 43). The cause of the excited state of these fish in group A2 is unknown but may be due to their bodies coming into contact with the glass as they entered the flask. It thus seems that the state of excitation of the fish is an important factor governing gas release.

In group C, 2 observations were made at reductions of 0.26 cm Hg/sec and 4 between 0.13 and 0.17 cm Hg/sec. The mean percentage pressure reduction for these 6 fish was 25.3% ($s = 5.3$) which did not differ significantly from the mean based on fish in groups A1 and B tested at 0.1 cm Hg/sec ($t = 1.6$; d.f. = 44). Thus increasing the rate of pressure decrease within the range investigated did not influence the pressure reduction causing gas release.

B4. The Effectiveness of Gas Release

Method. The determination of the effectiveness of gas release in adjusting the volume of the swimbladder to a new reduced pressure was the starting point in a study, described in section C2 to which the reader is referred for details, on the recovery of buoyancy after gas loss. Thirteen herring which had fed on plankton and 16 non-feeding fish were subjected to a pressure reduction of −40 cm Hg on the manometer scale, a reduction of 49 to 52% from the pressure to which they were adjusted. This reduced pressure was maintained for half an hour then the herring were anaesthetized and their flotation pressure determined.

RESULTS. In section A3 it was established that neutral buoyancy was reached when the pressure had been reduced by a mean of 5.5% from the pressure of adjustment. As the total pressure at manometer −40 cm Hg was 40.4 cm Hg the herring if they had adjusted perfectly to it would be expected on this basis to have neutral buoyancy at a mean total pressure of 38.2 cm Hg. Any deviation of flotation pressure from this value is a measure of the failure of the fish to adjust to a pressure reduction of about 50% in half an hour. The 15 non-feeding fish tested had neutral buoyancy at a mean total pressure of 44.6 (s = 4.6) while the corresponding value for the 13 fed fish was 46.7 cm Hg (s = 4.5). Considering the results of these two groups together shows that the herring had come within 19% of perfect adjustment to the new pressure within half an hour. As the herring swimbladder has no gas glands it is assumed that most of this adjustment was due to the observed release of gas which began during pressure reduction and was completed in the first six minutes at 40.4 cm Hg.

B5. THE BEHAVIOUR OF HERRING DURING PRESSURE DECREASE

METHOD. Observations were made on the behaviour of herring undergoing pressure reduction from 80.4 cm Hg to 40.4 cm Hg at rates between 0.06 and 0.13 cm Hg/sec in the experiment described in section C2.

RESULTS. Typically the 142 herring observed remained throughout the pressure reduction in the lower half of the 60 cm deep carboy in which they were tested, swimming moderately and predominantly horizontally until their increasing buoyancy was reduced by gas release. None of the herring observed were carried helplessly up to the top of the carboy and none had to compensate for their increased buoyancy by vigorous swimming with the head down. As herring can compensate by moderate locomotory activity until gas is released it seems that there is no restriction imposed on the upward movements of herring by increased buoyancy. After gas release the herring were able to compensate easily for the slight excess buoyancy remaining during the half hour at 40.4 cm Hg.

The response of the herring to pressure decrease is such that it would tend to return the herring to its initial depth if herring were being lifted upwards by an upwelling current of water.

B6. SURVIVAL AFTER PRESSURE DECREASE

METHOD. Herring adjusted for 1 to 2 weeks to a total pressure of 82 cm Hg were compressed in a modified steam sterilizer fitted with a pressure control and an inflow of sea water under pressure. This sea water came to the experimental vessel in a closed system from a reservoir open to the atmosphere. The herring were taken from a total pressure of 82 cm Hg to 176 cm Hg and held at the higher pressure for 16 hours before decompression to 82 cm Hg. After decompression the herring were held for subsequent observation.

RESULTS. This experiment showed the survival of herring both after compression and after decompression as any fish which were alive at the end of the experiment must have survived both pressure changes. The results in Table II show that herring can survive a pressure increase of 115% from their adjusted

TABLE II. Survival of herring adjusted to 82 cm Hg, compressed to 176 cm Hg, held at this pressure for 16 hours and then returned to a pressure of 82 cm Hg.

Fish group	Number of fish	Average rate compression	Average rate decompression	Fish deaths		
				Time after decompression		
		cm Hg/sec	*cm Hg/sec*	0–5 *min*	0–24 *hr*	24–48 *hr*
A	6	2.2	62.8	0	0	0
B	6	4.9	54.2	0	0	0
C	6	1.8	62.5	0	0	0
D	6	2.6	57.2	0	0	0
E	6	5.7	123.5	0	1	0

pressure at a rate of 6 cm Hg/sec. The interpretation of the decompression data is less certain as it is not known how far the herring had adjusted to the total pressure of 176 cm Hg during the 16 hours before decompression. As the herring had no access to the surface during this period the results given in section C2 would suggest that little adjustment to the higher pressure occurred. Whether there was any adjustment or not it can be concluded that herring can withstand the less severe condition, that of a return to the level of adjustment at rates up to 123 cm Hg/sec after compression of 115% of the adjusted pressure. They can also survive this rate of decompression after 16 hours has been allowed for adjustment to the greater pressure, without a water/air surface, a condition found when herring undergo compression by moving downwards at sea.

B7. DISCUSSION: THE UPWARD MOVEMENT OF HERRING

This section has provided answers to some of the unknown features of the upward movement of herring outlined in the introduction. The posterior swimbladder duct is certainly functional in the herring and serves as the usual exit for excess gas during pressure decrease. It is an efficient means of adjusting buoyancy when the herring rises, as it can bring the herring to within 19% of perfect adjustment to the new pressure within half an hour after a pressure decrease of 50% of the adjusted pressure. Through their behaviour herring were able to compensate easily for their excess buoyancy during pressure decrease at 0.13 cm Hg/sec (which corresponds to 10%/min) until their buoyancy was reduced by gas loss. Thus herring rising at a rate of 11 m/min at 100 m depth; at 6 m/min at 50 m or at 2 m/min at 10 m would have no limit placed on the extent of their upward movement by too great an increase in buoyancy or through rupture of the swimbladder. In this respect they differ from physoclists which have an upper limit to their range which can only slowly be lifted by absorption of the excess gas. The direct, functional connection between the swimbladder and the exterior may also give the herring an advantage in this respect over other physostomes which liberate gas less directly through pneumatic duct, oesophagus and mouth.

C. THE HERRING SUBJECTED TO PRESSURE INCREASE

C1. Introduction

Herring moving downwards from the depth at which they are adjusted increase in density as the increasing pressure compresses the swimbladder gas. A limit to this downward movement might be imposed by the ability of the herring to compensate by locomotory movements for its increased density until buoyancy was restored. As the compensatory movements involve an expenditure of energy the time element is obviously of importance.

The duration of the compensatory movements depends on the speed with which the herring can become adjusted to its new depth by increasing the mass of gas in the swimbladder. In the Clupeidae numerous capillaries occur in the thickened epithelium over the forepart of the swimbladder wall but they do not merge to form retia mirabilia (Jones and Marshall, 1953). Thus, anatomically, the herring swimbladder does not show the modifications for extensive gas secretion and resorption found in physoclists and a few of the physostomes. This raises the question of how, if at all, herring down from the surface by day become adjusted to the increased pressure.

C2. Restoration of Buoyancy

Material. One hundred and forty two herring initially adjusted to pressures of 78 to 84 cm Hg were tested in groups of 5 to 16 fish.

Apparatus and method. The herring were tested in a carboy 60 cm deep with a capacity of 51 litres (Fig. 4). The carboy was connected to a pressure reservoir and manometer and the pressure reduced from 80.4 cm Hg to 40.4 cm Hg at a rate between 0.06 and 0.13 cm Hg/sec. The herring were held at a total pressure of 40.4 cm Hg for half an hour before returning to 80.4 cm Hg. The control fish were immediately anaesthetized and the pressure at which each fish had neutral buoyancy was recorded. All other fish groups were allowed a period for recovery of gas lost during the decompression, during which they were held at atmospheric pressure in water continuously renewed with bubble-free sea water. In addition some groups were given access to the surface by lowering the water level to the shoulders of the carboy; or were given a fine stream of air bubbles from an aerator or were fed on plankton. Most fish spent their recovery period in the carboy but 6 of the 32 fish fed on plankton were allowed to recover without access to the surface in a stock tank of the same depth as the carboy. At the end of the recovery period the fish were anaesthetized and the pressure of neutral buoyancy of each fish determined. Final results were only obtained for 84 of the 142 fish tested as the rest liberated gas before neutral buoyancy was reached.

Results. The mean pressures at which the fed and unfed control groups (lots 1 and 2, Table III) had neutral buoyancy did not differ significantly from each other ($t = 1.2$; d.f. $= 26$) so the results of the two groups were combined and the mean pressure of 45.6 cm Hg ($s = 4.7$) so obtained was used as a standard against which the recovery of buoyancy by the other groups could be tested.

No recovery of buoyancy was shown by the group of herring kept in running, bubble-free sea water for 24 hours (lot 4, Table III). This suggests that

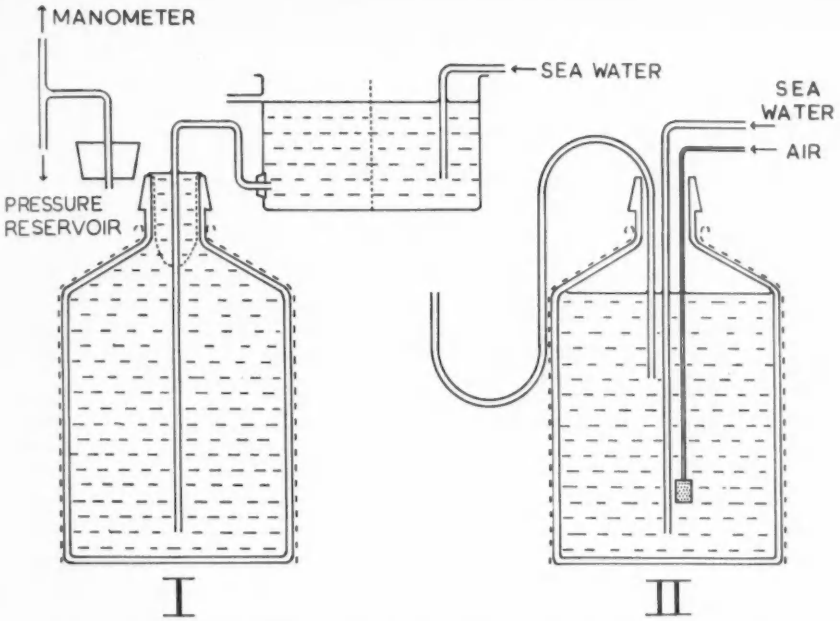

FIG. 4. Apparatus used to investigate the recovery of buoyancy by herring after gas loss.

the ability of herring to secrete gas into the swimbladder is very poor, a condition that might be expected from the lack of retia mirabilia. Even when fine bubbles of air were present in the water herring did not chase after or capture them and such fish showed no significant recovery over 24 hours (lot 5). A recovery, significant at the 0.1% confidence level ($t = 7.8$; d.f. = 38), was found when the herring had access to the surface (lots 6 and 7). These fish thrust their heads through the surface as soon as the pressure was returned to atmospheric and bubbles of air left their mouths when they swam down again. Two of the 9 fish tested in lot 7 had recovered buoyancy to such an extent that they floated at atmospheric pressure when anaesthetized.

It proved difficult to determine the recovery of buoyancy by fish fed on plankton (sometimes with mud from the shore near a sardine cannery added to provide bacteria), because not all herring fed under the conditions of the experiment. The results presented here apply to fish of which 78% had some food in the stomach when killed after the 24-hour recovery period (lots 8 and 9, Table III). No recovery of buoyancy by the 32 fish tested was indicated by the mean value based on the whole group, or by mean values based on the 11 fish caught 2 to 3 hours before testing (lot 9), or on the 21 fish held in captivity (lot 8). However among the latter there was one group of 6 tested fish which had a mean pressure of neutral buoyancy of 52.0 cm Hg ($s = 6.1$) which differed significantly (0.1% confidence level) from the mean of the control group ($t = 5.5$, d.f. = 32).

TABLE III. Recovery of gas loss by herring returned to a total pressure of 80.4 cm Hg after half an hour at 40.4 cm Hg, shown as changes in the mean pressure of neutral buoyancy. (s = standard deviation of individual observations.)

Lot no.	Fish used	Test conditions	Pressure at neutral buoyancy	
			Mean	s
			cm Hg	*cm Hg*
1	15 unfed	Immediate test	44.6	4.6
2	13 fed	Immediate test	46.7	4.5
3	4 unfed	4 hr in bubble-free sea water	40.3	0.6
4	6 unfed	24 hr in bubble-free sea water	42.6	3.5
5	5 unfed	24 hr in aerated sea water	42.3	2.9
6	3 unfed	24 hr in aerated sea water with access to surface	65.2[a]	5.0
7	9 unfed	24 hr in bubble-free sea water with access to surface	65.0[a]	12.0
8	21 fed	24 hr in bubble-free sea water with plankton	46.6	6.6
8a	6 fed[b]	As above, but also fed heavily ¼ hour before the experiment	52.0[a]	6.1
9	11 newly caught, fed	24 hr in bubble-free sea water with plankton	47.1	4.1
		Summary		
1, 2		No recovery time	45.6	4.7
3		4 hr no access to surface	40.3	0.6
4, 5		24 hr no access to surface	42.5	3.3
6, 7		24 hr access to surface	65.0[a]	10.7
8, 9		24 hr with food	46.7	5.9

[a] Means so marked are significantly greater than the combined control mean of 45.6 at the 0.1% probability level.
[b] These 6 fish are included in lot 8, above.

This group while in the stock tank had been fed occasionally on plankton, and half an hour before the start of the experiment was given a large amount of mainly copepod plankton but no mud from the sardine cannery. This was the only group in which a large quantity of red faecal matter was present in the carboy after the 24-hour recovery period. Of the 10 fish present in this group (neutral buoyancy could only be determined for 6) 5 had gas and food in the stomach, 2 had only gas and 3 had only food. The existence of this one group which showed significant recovery of buoyancy when fed on plankton suggests but does not establish that under certain conditions herring buoyancy may be restored by bacterial gas-producing activity in the stomach.

From the results obtained the effectiveness of gas release in bringing the herring in equilibrium to a new reduced pressure can be determined and this is discussed in section B4. The behaviour of the herring during pressure increase and decrease in these experiments is discussed in sections B4, B5, C3 and C5.

C3. The Behaviour of Herring during and after Pressure Increase

OBSERVATIONAL GROUPS. In the experiment on the recovery of buoyancy described in section C2 there were 43 fish which made no significant recovery over 24 hours. These fish had neutral buoyancy at a mean value of 45.7 cm Hg which is equivalent to perfect adjustment to a total pressure of 48.4 cm Hg. Thus these

fish whose recovery period was spent at a pressure of 80.4 cm Hg had been held at a mean pressure increase of 66% from their adjusted pressure for 24 hours.

Herring behaviour during increasing pressure was also observed by underwater television in groups of herring held in a cage at sea and lowered to 100 feet (Brawn, 1960a). These herring had been held for several hours in a shallow tank before testing and presumably were adjusted to pressures within a few feet of the surface. A descent to 100 feet (30 m) subjected the herring to a pressure increase of about 300% from their adjusted pressure.

Results. In the laboratory experiments the herring were subjected to an almost instantaneous increase in pressure of an average of 66% of the pressure to which they were adjusted. Immediately after the pressure was increased the herring invariably swam to the top of the carboy and remained there swimming vigorously with their heads upwards. After 4 minutes one group observed still had many fish swimming with their heads upwards although by then the fish were evenly distributed in the carboy. This response to pressure increase would tend to bring up herring which sank below their level of adjustment. These herring showed no recovery of buoyancy during the 24-hour test period yet were still swimming normally at the end of that period. Thus, herring are able to compensate by locomotory activity for at least 24 hours for their increased density following pressure increases of 66% from their adjusted depth.

Herring lowered from the surface at sea swam normally during observations lasting 16 minutes at 100 feet, a pressure increase of 300%; and also for 1 hour at 60 feet (18 m), a pressure increase of 180% from the adjusted pressure. During the descent the herring swam mainly horizontally.

C4. Survival after Pressure Increase

Method. Herring adjusted to within a few feet of the surface were lowered in a cage at sea to a depth of 150 feet (46 m) giving a rate of pressure increase of 4 cm Hg/sec. At 150 feet the pressure was 430% greater than the total pressure to which they were adjusted. After 5 minutes the herring were returned to the surface and held for subsequent observation. During ascent the rate of pressure decrease was 5 to 6 cm Hg/sec.

Results. All herring swam normally from the moment they returned to the surface and no deaths occurred in a group of 58 fish in 1 hour or in a group of 86 fish in 2 hours.

C5. Discussion

The experimental evidence shows that herring given access to the surface take in air through the mouth and are able to increase their buoyancy by this means so that they are again adjusted to surface pressure. As the ability of herring to secrete gas into the swimbladder over 24 hours was shown to be negligible, it appears that if herring are to become in equilibrium with any pressure below the surface that they must carry down air with them from the surface.

Another more remote possibility for herring which have fed heavily on plankton is that gas generation by bacteria may be a subsurface source of swim-

bladder gas. A bacteriological study of herring from the east coast of Canada and New England centered on the Passamaquoddy region was made by Obst (1919). She showed that two types of gas-producing bacteria, one *Bacillus walfischrauschbrand* and the other unidentified, may be present in the gills and digestive tracts of living herring. All bacteria appeared to be eliminated from the digestive tract in the absence of food but almost invariably there were spores of *B. walfischrauschbrand* in the gills which could act as a reservoir of infection for the next food intake. This bacterium was commonly present in the schizopods on which the herring feed, in waste from herring canneries and in herring faeces. The second bacterium, called *Bacillus B* by Obst, was nearly always found on copepods which are also food for herring. Thus, the possibility of reinfecting the stomach contents with these bacteria every time the herring fed on plankton was excellent. In nearly all the fish that had taken copepod and schizopod food bacteria capable of producing gas were found, but 3 herring whose food consisted of small fish were free of bacteria in the stomach. When these 2 bacteria were cultured on the food on which they were found both produced gas abundantly at 37° and at room temperature when cultured on schizopods. Thus Obst's results suggest that bacterial gas production might be a source of gas for the swimbladder in herring which had fed on copepods or schizopods.

If this supposition should be correct it would provide a functional explanation for the unusual position of the pneumatic duct in herring. This duct, which passes between the posterior end of the stomach caecum and the swimbladder is well placed for the movement of gas generated in the stomach to the swimbladder. It is not so well placed as the normal oesophageal position for the movement of swallowed air into the swimbladder, especially when the herring has been feeding heavily and any air swallowed has to pass through the food mass in the caecum before reaching the pneumatic duct.

Under laboratory conditions it was not possible to demonstrate the production of swimbladder gas by this means except possibly in one group out of the 6 groups tested. This mechanism at this time should thus be regarded only as an interesting possibility whose validity has yet to be established.

D. HERRING UNDER NATURAL CONDITIONS

D1. Introduction

The depth to which herring in nature are adjusted cannot be determined by direct observations of herring at sea because of the ease with which they compensate during locomotion for wide departures from their adjusted pressure. If the herring are captured their buoyancy at atmospheric pressure can be established by immediately anaesthetizing them.

The release of gas bubbles by herring is observed under natural conditions. On the European coast gas bubbles are used as a sign of ascending clupeoids (Verheijen, 1956) and these are also observed from herring on the Atlantic coast of North America.

D2. Buoyancy and the Presence of Gas in the Intestine

Method. The brush weir method of fishing in the Passamaquoddy region provided herring in suitable condition for testing. These weirs are fished with a seine, which when pursed from below and slowly hauled brings the fish to the surface. Herring were surrounded by a large dip net, caught in a bucket of water and immediately anaesthetized with MS222.

Results. No release of gas by the fish was observed during seining nor during the transfer of fish to the anaesthetic. The weir at low tide when seined has a maximum depth of 25 feet. No fish were seen within 10 feet of the surface until the seine was closed and most fish were probably within a few feet of the bottom. When anaesthetized 25 of the 28 herring tested were positively buoyant at atmospheric pressure, the other 3 sank to the bottom. When dissected 17 fish had gas in the stomach caecum and all 28 had been feeding on copepods which were more dense than sea water. Of the 3 fish which were not buoyant at atmospheric pressure, 2 had gas in the stomach suggesting that their greater density was due to a less-than-normal volume of gas in the swimbladder.

D3. Discussion

Herring usually feed near the surface by night, returning to greater depths by day. If the herring tested at the weir had adjusted their buoyancy to that at the surface they would not have floated when tested at atmospheric pressure. Thus their observed buoyancy shows that they were in neutral buoyancy at some unknown depth below the surface.

E. GENERAL DISCUSSION OF THE RELATIONSHIP OF HERRING TO PRESSURE

E1. Pressure Relationships Associated with Diurnal Vertical Movements

A study of the vertical movements of herring in Passamaquoddy Bay, N.B., showed that the fish are nearer to the surface by night than by day in every month of the year (Brawn, 1960b). In February, typical of the first quarter of the year when vertical movements are greatest, the herring would experience a 113% increase and a 53% decrease of the initial pressure when moving between the median day and night depths. From May until December, assuming that the herring came to the surface at night the pressure increase would be between 91 and 133% and the decrease between 48 and 57%. The rate of pressure change in either direction was about 0.003 to 0.006 cm Hg/sec. Fairly similar pressure decreases (66%) are experienced by herring round the coasts of Scotland but there the pressure increases (380%) may be greater (Blaxter and Parrish, 1958).

Herring can compensate by locomotory movements for at least a 300% increase in pressure and can compensate during pressure decrease until their buoyancy is reduced by gas release. Thus the observed diurnal cycle of pressure changes could be undertaken by herring which were initially in hydrostatic equilibrium with their environment either at the surface, at the greatest depth

reached or at some intermediate depth. If they were in equilibrium at the greatest depth, the pressure decrease as they rose toward the surface at dusk is greater than the observed mean pressure decrease of 32% causing gas release generally so that herring would lose gas during the ascent. To maintain the cycle, this gas would have to be replaced within 24 hours and the experimental evidence suggests that this could only occur at the surface by air swallowing with, under certain circumstances, the possibility that this would be augmented below the surface by bacterial gas production. On theoretical grounds it seems unlikely that the herring would take in enough air at the surface to give neutral buoyancy at the greatest depth for this would necessitate having twice the normal mass of gas inside the body at the surface in order to have neutral buoyancy after a 100% pressure increase. Under such a regime the herring would have to compensate for its excess buoyancy at all points in the pressure cycle except at the greatest depth. It seems more likely that the herring would adjust in this manner to some intermediate depth to minimize the energy expenditure in compensatory movements.

There remains the possibility that herring adjust only to surface pressure and compensate for their increased density at greater depths. However, when the buoyancy of herring taken straight from the sea was tested (section D) it was found that the herring were adjusted to pressure at some unknown distance below the surface. In addition the observed release of gas bubbles from herring at sea, which experimental evidence has shown to be a consequence of herring experiencing a reduction in pressure from their pressure of adjustment, also suggests that in nature herring are adjusted to pressures greater than surface pressure. A suggestion can also be made about the intermediate depths to which the herring might be adjusted. As gas release in the laboratory occurred at a mean pressure decrease of 32% from the adjusted pressure the release of gas at sea suggests that herring must occasionally be adjusted to depths far enough below the surface, that is below 16 feet, for such a percentage pressure decrease to be encountered. As they can compensate for excess buoyancy until gas release they would also be able to take gas down from the surface in sufficient quantity to give neutral buoyancy at depths at least as great as this.

On the basis of this discussion it is suggested that herring by day are adjusted to some intermediate depth and while at depths greater than this compensate by locomotory activity for their increased density. As herring rise toward the surface at night gas may be released if the pressure decrease involved is greater than 32% of the adjusted pressure. At the surface the herring have a slight excess buoyancy, either because there was no gas release or because gas release does not bring herring into perfect adjustment to the new reduced pressure. Sometime during the night, either continuously or just before the descent at dawn, air would be swallowed increasing the buoyancy of the fish. This excess buoyancy would be compensated for until the herring descended. During the day air in the stomach and any bacteria-generated gas would pass slowly from the stomach caecum to the swimbladder, a movement which, while not increasing the buoyancy of the fish, increases stability by moving the centre of gravity

downwards. Below the depth of neutral buoyancy the herring would have to compensate for its excess density and so would continue until the ascent at dusk initiated the cycle of pressure and buoyancy changes again.

E2. Pressure Relationships Associated with Passage through Turbines

Under the proposed Passamaquoddy Power Project large, slow-moving turbines may be installed in the Passamaquoddy region to generate electrical power from the movement of sea water from a high to a low-level pool. Herring passing through these turbines would encounter rates of pressure change greatly in excess of those encountered in nature. *In the following discussion the pressure changes which would be experienced by a herring passing through the turbines on the centerline under conditions of mean water level are given first, with the most extreme values given in brackets afterwards.*

If the herring came in at the average depth of the channel to the powerhouse they would not be subjected to a change in pressure on entering the intake tube. In passing through the turbines the herring would pass from a total pressure of 143 (168) cm Hg in the intake; to 76 cm Hg at the top of the draft tube; to 221 (267) cm Hg at the bottom of the draft tube and finally to 175 (147) cm Hg at the draft tube exit (Trites, 1961). The maximum rate of pressure decrease of 36 cm Hg/sec lasting only 1 or 2 seconds would be encountered at the top of the draft tube. The second period of pressure decrease, as the herring ascended the rising limb of the draft tube, would occur at a rate of 3.1 (8) cm Hg/sec. In both situations the herring are subjected to rates of decompression less than those which they were shown experimentally (section B6) to withstand without subsequent mortality. In the first instance the herring might be adjusted to the initial pressure of 143 cm Hg but the percentage pressure decrease of 47% is within the range of pressure decreases withstood by some of the fish before gas release described in section B3, and thus should not be injurous to the fish even if the pressure change were too rapid for gas release. In the second instance herring rising up the draft tube are approaching their level of adjustment rather than moving away from it and so should not suffer ill effects from the decompression.

The herring would experience an increase in pressure of 178% (237%) in the descending limb of the draft tube at a mean rate of 19 (25) cm Hg/sec. Herring have been shown to survive pressure increases of this magnitude (section C4) but not at this rate. However, as pressure increase causes a decrease in the volume of the swimbladder gas it is not expected that compression at this rate would harm the herring. Thus, it seems that pressure changes alone would not cause mortality in herring schools that pass through the turbines. However, the herring is readily abraded and some mortality may be expected from those fish which come into contact with hard surfaces as they pass through the turbines.

SUMMARY

1. The physical and functional characteristics of the swimbladder were investigated using living herring 11 to 20 cm long from Passamaquoddy Bay, N.B.

2. Herring assumed to have adjusted to the total pressure of 78.6 cm Hg at the bottom of the holding tank had a mean sinking factor of 1003, density of 1.026 g/ml, percentage volume of swimbladder of 4.2 and relative sensitivity of the swimbladder of 0.8. Such fish had neutral buoyancy when the pressure was reduced 5.5% on the average from the pressure of adjustment. The mean excess pressure of the swimbladder gas was 1 cm Hg.

3. Herring have a posterior swimbladder duct which opens directly to the exterior and this served to release gas in 105 of 109 herring observed. Gas release in rapidly swimming fish occurred at a mean pressure reduction of 6.4% ($s = 2.6$) from the adjusted pressure compared with a reduction of 32% ($s = 9.8$) in moderately swimming fish. There was no significant difference in the mean pressure causing gas release during decrease at 0.1 cm Hg/sec and that during decrease at 0.13 to 0.26 cm Hg/sec. Following a pressure decrease of 49 to 52% the herring came to within 19% of perfect adjustment to the new pressure by gas release within half an hour. Gas release was completed within 6 minutes of arriving at the new reduced pressure after reduction at rates between 0.06 and 0.13 cm Hg/sec. Five herring were observed to release gas through the mouth.

4. During pressure decrease at 0.06 to 0.13 cm Hg/sec herring were able to compensate during locomotory activity for their increased buoyancy until this was reduced by gas release. After 16 hours at 176 cm Hg, decompression to 82 cm Hg at rates up to 123 cm Hg/sec did not cause subsequent mortality.

5. Herring more dense than their environment did not show significant increase of buoyancy over 24 hours when held in renewed sea water even if a fine stream of air bubbles was present. Herring showed significant recovery of buoyancy under these conditions if they had access to an air-water interface. Considered as a whole, herring which had fed on plankton showed no recovery when denied access to the surface, but one group of 6 herring out of the 6 groups tested showed significant recovery of buoyancy under these conditions. The tentative suggestion is made that gas-secreting bacteria in the stomach of herring may be a source of swimbladder gas in herring which have fed on plankton.

6. Herring could compensate while swimming for their increased density following pressure increase of 66% over 24 hours, of 180% over 1 hour and of 300% for 16 minutes. These times do not indicate the limit of the herring's ability to compensate as in all instances the fish were still swimming easily at the end of the observation period. Herring responded to a rapid pressure increase of 66% by swimming upwards. Herring survived a pressure increase of 430% at the rate of 4 cm Hg/sec without mortality.

7. Of 28 herring taken from the sea between 10 and 25 feet deep, 25 were positively buoyant at surface pressures when anaesthetized. This indicates

that at sea, herring are adjusted not to surface pressure but to some unknown depth below the surface. All of these herring tested had fed heavily on copepods. Gas was present in the stomach caecum of 17 fish.

8. It is suggested that herring in nature restore buoyancy lost by gas release by taking air in through the mouth when feeding at the surface by night and passing this through the pneumatic duct to the swimbladder. Enough air is probably taken in to give neutral buoyancy at some intermediate depth rather than at the greatest depth reached by day. If gas of bacterial origin is produced this would increase the depth of neutral buoyancy in plankton-feeding herring.

9. Passage through the turbines proposed by the Passamaquoddy Power Project is not expected to cause herring mortality through pressure changes. There may be some mortality under these conditions through abrasion of the fish.

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Quantitative Estimations of Temporal Variations of Zooplankton off the Coast of Washington and British Columbia[1,2]

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ABSTRACT

Quantitative sampling off the coast of Washington and British Columbia shows a regular seasonal variation of zooplankton volumes. Average volumes for the upper 200 meters of water in this area varied from a winter minimum of 0.035 cc/m³ in December 1956 to a maximum of 0.139 cc/m³ in May 1957. *Pseudocalanus minutus* (Krøyer) and *Oithona similis* Claus were the most numerous zooplankters; *Acartia danae* Giesbrecht was found to be potentially important as a species indicative of intrusion of near surface waters from the south.

Washington coastal waters yielded zooplankton volumes (1) approximately four to five times those reported for the equatorial Pacific, (2) similar to those recorded for the Gulf of Alaska, but (3) less than those reported in comparable areas of the northwestern Pacific.

The "normal" population of the area has not been established. The fact that in February 1958 the zooplankton populations were entirely different from those found a year earlier demonstrates the need for further study to determine long-term averages.

INTRODUCTION

The food potential of a given region is estimated by analyzing the temporal variation of the amount and type of marine zooplankton present in the standing crop. At present, quantitative samplings of zooplankton in the North Pacific Ocean are few. In particular, the northeast section, comprising the Gulf of Alaska and adjacent waters, has been neglected. McAllister has recently (1961) described vertical levels of zooplankton biomass concentrations at weather station "P" in south-central Gulf of Alaska.

However, most of the zooplankton studies in the area have either been taxonomic or limited to a few selected groups of organisms. Some copepods of the State of Washington inland marine waters have been investigated by Herdman (Herdman *et al.*, 1898) and major plankton forms by Johnson (1932). Summer plankton and Copepoda species of the Strait of Georgia and Vancouver Island were described by Campbell (1929a, 1929b). For the British Columbia

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coastline the taxonomy and regional distribution of four species of Chaetognatha has been described (Lea, 1955) and 32 copepod species have been identified by Cameron (1957) in the Queen Charlotte Islands area. Settling volumes of Copepoda in six British Columbia inlets (Lebrasseur, 1955) and a semiquantitative plankton study in the Strait of Georgia (Légaré, 1957) give an index to quantities in Canadian waters.

Preliminary descriptions of Copepoda of the Alaskan and Bering Sea area by Willey (1920) were followed by zooplankton community studies in the Bering Sea by Johnson (1934). Johnson later (1938, 1941) described the distribution of species of *Eucalanus* in the Northeast and North Pacific. A systematic study by Davis (1949) added 36 copepod species to the record for the eastern North Pacific area. Copepods of the general area were considered by Wilson (1942, 1950) and three species of Chaetognatha have been described in the Gulf of Alaska by Sund (1959).

Material collected for halibut egg studies in the Northeast Pacific by Thompson and Van Cleve (1936) and Van Cleve and Seymour (1953) was later used in taxonomic studies of Mysidacea and Euphausiacea by Banner (1947, 1948, 1950).

The present study was conducted as a preliminary survey to ascertain regional distribution and temporal variation of the common zooplankton groups found off the Washington-British Columbia coast throughout the year (Fig. 1). The results were correlated with fluctuations of measured oceanographic conditions. An attempt was made to occupy the same geographic station locations on every cruise but weather conditions sometimes prevented this and occasionally curtailed the program.

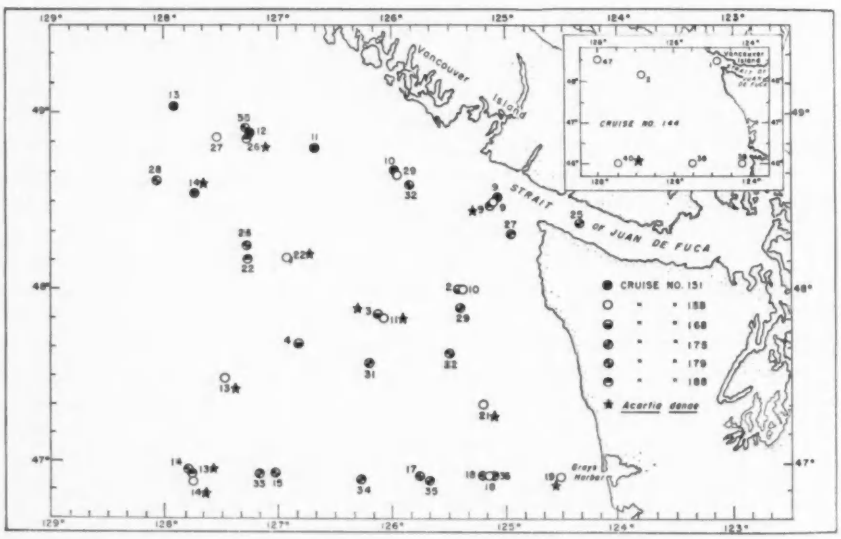

FIG. 1. Station locations for cruises taken in December 1956 (151), February 1957 (158), May 1957 (168), July 1957 (175), November 1957 (179) and February 1958 (188), plus insert of the cruise-144 stations taken in summer 1956 in the present area of study.

METHODS

The standard plankton sampling on each station consisted of oblique tows taken from 200 meters depth (depth permitting) to the surface, using modified (Paquette and Frolander, 1957) Clarke-Bumpus quantitative samplers with No. 6 mesh nets (0.239 mm mesh openings). For comparison, vertical hauls through the same depths were taken with half-meter nets of No. 6 mesh immediately following the Clarke-Bumpus hauls. Previous measurements have indicated that No. 6 mesh nets should be fine enough to catch developmental stages of such small representative copepods as *Acartia clausii* down through copepodite stage I.

The upper size limit of planktonic organisms sampled representatively by a No. 6 net or any other particular mesh is difficult to ascertain because it is determined not only by mesh size but speed of hauling, diameter and amount of clogging of net, as well as physiological state, degree of awareness, and agility of the organisms. The small opening of the Clarke-Bumpus sampler does of course put limitations on it with respect to its catching power of scarce or fast moving organisms, but at hauling speeds of one to three knots it should catch large copepods that occur in its immediate path. Wiborg (1948) made comparative tows with Clarke-Bumpus samplers in Norwegian fjords and noted in his discussion that there seemed to be "no great difference between the catches of the bigger copepods [*Calanus finmarchicus, C. hyperboreus*] in the net with silk No. 2 and those in the 11 net, and one way assume that the 11 net will give a quite reliable picture of the whole copepod population". The danger in using small nets is that an absence of rarer or very active species from the collection may be interpreted as a real scarcity or an absence from the community. Winsor and Clarke (1940) indicate that with the 12.7 cm diameter net of the type used on the Clarke-Bumpus sampler, the proportions of the various groups they sampled (including sagittae, amphipods and large copepods) did not vary in a manner to indicate preferential selection with net size although the data for *Sagitta* were inconclusive.

Using 75-cm scrim nets they derived a standard deviation of 31% for a single observation with oblique hauls in contrast to 53% for a single observation for vertical hauls of 30.5- and 75-cm nets. With respect to size of nets, zooplankton species collected in the present study would not be expected to behave markedly different during capture from those species (*Calanus finmarchicus, Centropages typicus, C. hamatus, Pseudocalanus minutus*) counted in the above study.

Bigelow and Sears (1939) suggest that the plus or minus error of calculated zooplankton volumes caught in silk nets (Nos. 00 to 2 mesh) towed at an assumed speed of 1.2 knots may average 20–30%, catching organisms from copepods such as *Centropages* up to fish fry. It was emphasized that such values were much smaller than the variations observed among the values forming the basis for the study and that the consistency of the samples indicated their representativeness for the larger zooplankton. Winsor and Walford (1936) cite literature

varying from 10 to 30% and higher for plankton catch variability in comparative hauls with similar nets.

In the present study the time between taking samples with Clarke-Bumpus sampler and half-meter net at any one station was never more than 26 minutes and at 75% of the stations was 15 minutes or less. All but two of the half-meter net vertical tows were hauled to the surface at speeds of 0.5 to 2.1 knots (0.9—3.9 km/hr); two exceptions were 2.4 and 3.2 knots (4.5 and 5.9 km/hr). From

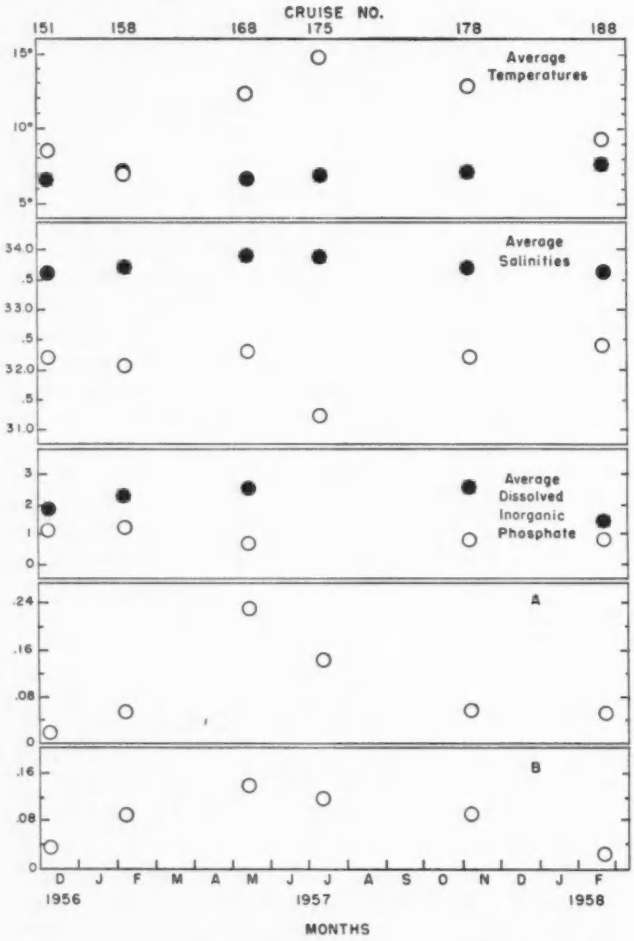

FIG. 2. *Top:* Average temperature (°C), salinity (‰), and dissolved inorganic phosphate (μg-at/liter) at the surface (open circle) and at 200m (solid circle) for each cruise. *Bottom:* Average zooplankton displacement volumes for half-meter vertical tows (A) and for Clarke-Bumpus oblique tows (B).

previous work one might expect possible variations from the calculated quantities for the half-meter net catches to be about 25% for individual hauls. However, comparison of the seasonal trend of volume averages of the latter catches for each cruise with those of the Clarke-Bumpus sampler shows reasonable similarity of volume and trend throughout the period of study (Fig. 2A, B)[4].

In the laboratory, all plankton samples were first examined under a dissecting microscope. Organisms larger than 4 mm in maximum diameter were identified, counted, and removed directly from the samples. The number of the remaining organisms was determined by counting the specimens extracted in a 1-cc aliquot with a Stempel pipette after diluting the sample settling volume 5 times. Subsequently, the displacement volume of each sample was determined in duplicate analyses using a plankton volume indicator (Frolander, 1957). The volumes of the water filtered by the Clarke-Bumpus samplers were determined through calibrations obtained by towing the instrument over a measured course; those of the water filtered by the half-meter net were determined by calculating the volume of water in the column sampled.

Numbers of the various types of organisms, and the displacement volumes of the total zooplankton per cubic meter of water filtered, were calculated and each of the chosen systematic divisions of organisms which represented at least 9.5% of the number of specimens in a sample was listed separately in Table I. Although never numerous, *Oithona spinirostris*[5] was also tabulated to indicate its continuous distribution; all remaining copepods, regardless of percentage, were listed together as numbers per cubic meter.

All temperatures quoted are Centigrade, except as noted.

RESULTS

A regular seasonal progression of zooplankton volumes is evident for the area (Fig. 2B). Minimum average displacement volumes of 0.035 and 0.025 cc/m^3 for the Clarke-Bumpus samples were recorded in December 1956 and February 1958 respectively. The maximum average of 0.139 cc/m^3 was recorded during the middle of May; volumes were lower during the summer.

Average volumes for each cruise determined from the half-meter net samples also show a regular seasonal progression of abundance (Fig. 2A). Indeed, there is good agreement, in time and relative abundance of the two winter minima and one spring maximum of plankton volumes, between catches by the two types of equipment (Fig. 2A, B).

Higher volumes were usually found in those samples taken nearer the coast (Fig. 1, Table I). Samples taken inside the hundred-fathom contour line, from December 1956 through November 1957, were compared with samples taken farther offshore during the same period. The average volume of the inshore samples was 0.15 cc/m^3 and that of the offshore samples, 0.08 cc/m^3. Although

[4]Standard records of temperature, salinity, oxygen, and phosphate, as well as of surface weather conditions, were taken at each station. These data will be tabulated in a forthcoming report.

[5]Special care was taken to distinguish the several species of *Oithona*.

TABLE I. Organisms taken in 6 series of samples. Columns 3-6 include organisms representing at least 9.5% of the specimens found in one sample or another of each series. T—a trace, less than 9.5%; A—adult stage; C—copepodite stage; D—day; N—night; (d)—some decomposition in sample; Vol.—displacement volume of sample; Max. depth—maximum depth of CB samples.

Organisms are as follows:
P. m. = *Pseudocalanus minutus*
O. similis = *Oithona similis*
M. l. = *Metridia lucens*
O. spinirostris = *Oithona spinirostris*
Other Cop. = other Copepoda

1 Station No.	2 Max. depth	3 *P. m.*	4 *O. similis*		5 *M. l.*	6 Others	7 *O. spinirostris*		8 Other Cop.	9 Volume	10 Time of haul
		A	A	C			A	C			
	m	no./m³	no./m³	no./m³	no./m³	no./m³	no./m³	no./m³	no./m³	cc/m³	
BB151. 5-10 December, 1956											
9	94	124	109	48	...	...	17	...	46	0.04	D
10	56	98	...	...	...	[a]	T	...	27	0.05	D
11	200	85	28	1	...	...	6	...	36	0.03	N
12	200	108	T	...	26	...	5	...	65	0.04	N
13	200	242	9	3	...	...	4	...	56	0.03	D
14	200	253	14	3	...	...	6	6	524	0.02	D
BB158. 4-11 February, 1957											
9	115	95	41	1	32	...	4	...	24	0.16	D
10	200	88	17	1	17	...	7	3	16	0.08	D
11	200	39	46	3	...	...	4	...	53	0.16	N
13	200	32	7	...	11	...	4	...	8	0.02	D
14	200	49	T	...	...	[b]	12	...	20	0.04	D
18	200	47	69	8	39	[c]	6	2	11	0.04	D
19	71	154	210	93	...	...	8	2	110	0.12	N
21	200	84	67	27	...	[d]	5	7	72	0.12	N
22	200	35	43	8	...	...	8	...	30	0.05	D
27	200	31	23	2	...	...	2	2	23	0.03	D
29	50	374	117	31	...	...	23	8	199	0.19	N
BB168. 13-17 May, 1957											
2	200	559	T	T	...	[e]	5	3	212	0.14	D
3	200	181	116	12	...	...	8	6	260	0.19	N
4	200	279	108	59	...	...	8	2	199	0.09	D
BB 175. 8-15 July, 1957											
25	200	408	T	T	...	...	4	...	684	0.24	D
27	200	84	48	5	...	...	2	1	188	0.40	N
29(d)	200	...	142	39	...	...	22	13	702(d)	0.03	D
31	200	146	46	31	...	...	30	26	427	0.07	D
33	200	91	46	149	...	...	31	22	215	0.06	D
34	200	189	T	T	...	...	4	3	205	0.03	D
35	200	72	33	13	...	...	12	8	48	0.07	D
36	200	38	65	25	...	[f]	15	13	115	0.05	N
BB 179. 4-12 November, 1957											
14	200	...	42	131	...	...	5	2	145	0.06	N
15	200	...	19	608	...	[g]	19	...	412	0.11	N
17	200	...	50	101	...	...	6	3	171	0.10	D
18	200	...	21	20	...	...	7	6	133	0.06	N
22	200	...	32	9	...	...	5	1	212	0.10	D
26	200	...	35	350	...	[h]	22	13	167	0.08	D
28	200	...	22	9	...	...	7	3	133	0.12	N
30	200	...	46	186	...	...	6	3	171	0.12	D
32	40	45	12	4	...	[i]	T	1	71	0.09	N
BB 188. 19-28 February, 1958											
9	100	...	T	...	...	...	3	2	108	0.03	D
13	200	...	15	8	...	[j]	5	9	99	0.02	D
22	200	...	T	...	...	[k]	3	2	53	0.03	D
26	200	...	T	T	...	[l]	1	T	33	0.02	D

[a] 28 *Corycaeus* sp. [b] 16 *Eucalanus bungii*. [c] 25 *Calanus* sp. [d] 39 *Calanus* sp.
[e] 266 *Acartia longiremis*. [f] 38 Unidentified eggs. [g] 463 Larvacea. [h] 135 Larvacea.
[i] 28 *Corycaeus* sp. [j] 52 Sarcodina. [k] 20 Sarcodina [l] 6 Sarcodina.

the largest single volume for each cruise was usually recorded for a night station, volumes almost as large were recorded for daylight stations (Table I). Day-night variation in volume was less evident during the period of winter minimum in December 1956 (Table I). However, comparisons of average day-night variations are deceptive since the larger night catches by chance were taken near the coast where volumes were usually higher.

The zooplankton samples were dominated numerically by the copepod species *Pseudocalanus minutus* (Krøyer)[6] and *Oithona similis* Claus. These copepods were found in most samples from December 1956 through November 1957. In February 1958 they were few, and no *Pseudocalanus* were found at the southwesternmost station. In December 1956, *Pseudocalanus minutus* was the most abundant species at all except the most inshore station. By February their numbers had increased, particularly near the coast. The highest concentration, of more than 500/m^3, was recorded in May 1957, when *Pseudocalanus* dominated all other copepods. During the summer, the species continued to be abundant, but by November a decrease was evident (Table I).

Two cyclopoid species of copepods were commonly found during the entire sampling period. *Oithona spinirostris* Claus was recorded at all stations sampled and *Oithona similis* Claus was missing from only one station, 151-10, in December 1956. Adults and copepodites of *Oithona similis* usually greatly outnumbered *O. spinirostris* at each station, many times by a factor of 10, and exceeded 600/m^3 during the period of maximum recorded in November 1957. The maximum numbers of adult and copepodite stages of *O. spinirostris* were recorded during July, reaching approximately 50/m^3; for the other 5 cruises, numbers of this species were usually less than 15/m^3. Males of the genus were rarely encountered in any sample.

The usual lack of male specimens of *Oithona* in the samples may indicate their scarcity in the water but it is of interest to note that the dimension at the point of maximum width of the thorax of the male specimens measured was approximately the same as the size of the mesh openings of the nets used (0.239 mm); the few males taken, most of which were *O. similis*, may have been only those which did not escape through the mesh. However, corresponding measurements of *O. similis* females were very similar to the males, thus the sex ratios observed may have been as accurate as could be expected from sample size. Finer mesh net catches should be taken in the future to check the numbers of the sexes of these species present in this area.

[6]Specimens of *Pseudocalanus* from 14 stations of cruises 151, 158, 168, 175 and 179 were very kindley examined by Dr Thomas E. Bowman, Division of Marine Invertebrates of the Smithsonian Institution. He pointed out that it has been the practice to lump all members of the genus into a single species, *P. minutus* (Krøyer), with the forma or subspecies *elongatus*, *major*, and *gracilis* and that With (1915) lowered the status of the three species recognized by Sars (1900, 1901–1903) because he found intermediate forms, and most workers have followed him. Dr Bowman believes that the systematics of *Pseudocalanus* must be thoroughly investigated on a world-wide basis before it can be determined whether With was correct. Almost all of the specimens examined from the present study were provisionally identified as belonging to *P. gracilis* Sars characterized by the protruding forehead, long antenna, and slender body and legs. The cephalothorax was about 2.0–2.2 times as long as the urosome, while in *P. elongatus* this ratio is 2.4–2.5. The specimens examined were noted as unquestionably different from Atlantic specimens of *P. minutus* and were placed on deposit in the Smithsonian collection by Dr Bowman.

Using Olson's (MS, 1949) criteria, *Oithona spinirostris* was identified by the presence of the small papilla on the ventral aspect of the fifth thoracic segment of the female and the absence of hairs on the genital segment which differentiates it from the mature *O. plumifera* female. The latter lacks the papilla, but has hairs on the genital segment.

In separating these species, none of the large female specimens was ever observed with hairs on the genital segment, but the thoracic papilla was found on most specimens examined. Because of the warmer temperature ranges found for *Oithona plumifera* by Olson (MS, 1949) and the absence of mature females of this species in the present sampling, in addition to the presence of mature females of *Oithona spinirostris*, it was assumed that the copepodite females of these two species which might be readily confused were primarily *O. spinirostris*.

Olson (MS, 1949) working between latitudes of 25° to 45° N and east of Longitude 130° W along the west coast of North America never found *Oithona plumifera* Baird at any station where the surface temperature was less than 16°, whereas the range of *O. spinirostris* extended to the most northern station in the series. Both species occurred at 4 stations with temperatures of 16° or higher but *O. spinirostris* was noted as absent at all stations with surface temperatures warmer than 18°. The data, taken during the period May 10 to July 10, 1939, show no *O. plumifera* found north of latitude 36° N.

Four stations of the present series, 175–31, 175–33, 175–34, and 175–35 had surface temperatures of 16° or higher, but no mature *Oithona plumifera* were found.

The only other species of copepod which contributed appreciably to the catch was *Acartia longiremis* (Lilljeborg). This species was most abundant during May, and at the most inshore station (Fig. 1, Table I). The species also appeared in December 1956, and February and July 1957. The numbers were highest inshore and decreased to seaward.

Only three other groups of organisms (Larvacea, Chaetognatha, Euphausiacea) were sporadically captured in appreciable quantity. Larvacea occurred commonly only in November when members of the genus *Oikopleura* were present at all but the most western station and showed a decreasing gradient of 463 to 28 per cubic meter, from south to north at a series of 3 stations (15, 26, 30) an intermediate distance from shore[7].

Although separate volume analyses were not made of the low numbers of Chaetognatha and Euphausiacea recorded at certain stations, it was apparent from visual inspection of these preserved samples that they contributed appreciably to their total volumes (Stations 158–9, 11, 19, 21; 168–2, 3; 175–27).

DISCUSSION

Seasonal Variation

The Copepoda are the abundant forms with but two species, *Pseudocalanus minutus* and *Oithona similis*, constituting the majority of the catch. The increase in average volume to the maximum recorded in May is due largely to

[7]The respective Clarke-Bumpus cyclometer readings of 174, 184, and 70 revolutions per minute give no evidence of unusual net clogging due to these organisms.

the greater abundance of the same species which are present earlier in the year, particularly *Pseudocalanus minutus*. The record of the May period of maximum for this species corresponds with data for the central area of Puget Sound (Hebard, MS, 1956). Compared with the population in May, the population of *Oithona similis* in July has relatively increased as it gradually replaces *Pseudocalanus minutus* in importance. By November 1957, *Oithona similis* far outnumbers the other species. This process is most evident at the stations farthest from shore (Table I, Fig. 1). Although too few data are available to warrant conclusive findings, it is of interest to note that a comparison of samples taken inside the 100-fathom contour line with those taken farther offshore possibly indicates a different range of seasonal change for the two regions. In inshore waters, July was the period of maximum average zooplankton volume. This average, 0.32 cc/m^3, is more than 6 times the average volume for the offshore water in the same month. In offshore waters, the maximum average volume, about 0.14 cc/m^3, was recorded in May. No data were taken in inshore waters on the May cruise.

The minimum average volumes for both inshore and offshore waters were recorded in December 1956 and February 1958. In December 1956, the inshore and offshore areas yielded volumes of 0.047 and 0.029 cc/m^3, respectively; in February 1958, volumes of 0.029 and 0.024 cc/m^3, respectively.

Zooplankton populations at Canadian weather station "P", Latitude 50°N, Longitude 145°W, reported for the period December 1956 through January 1958 by McAllister (1961) show an average biomass pattern which in the main is remarkably similar to concentrations found off the Washington coast for the same period despite the differences in equipment, mesh of nets, and type of haul. Derived[8] monthly averages for McAllister's data for March 1957 to January 1958 show a winter-early spring minimum ranging from approximately 0.025 to 0.040 cc/m^3 (with one exceptionally low March sample excluded), a maximum of approximately 0.1 to 0.2 cc/m^3 May to July and summer values from approximately 0.03 to 0.06 cc/m^3 for the 0–200 meter vertical net tows. McAllister (1961) notes that although highest concentrations were observed in May for the 0–150 meter layer, where the most vertical tows were taken, the trends suggest that the maximum was reached in June in the interval between two periods of observation. The species were not listed, but vertical hauls contained mainly copepods throughout the year, with larger species abundant in shallow hauls (above 200 m) only during April and May, after which they were taken mainly in deep hauls (300, 500, 1000 m).

Comparison with Other Data

In zooplankton quantities, reported by Nakai (1952) in grams wet weight, the waters south to east of Kamchatka Peninsula are somewhat higher than those off the Washington coast. For comparison, data derived from samples taken by

[8]Samples were averaged by months in grams of zooplankton per cubic meter and multiplied by the reciprocal of 0.62 to convert grams to cc/m^3; the value 0.62 for conversion from cc to grams of zooplankton was utilized by McAllister (1961) as determined from Bering Sea data (Hokkaido University, 1957).

Nakai with a 45-cm net (0.3-mm mesh) in vertical 150-meter depth hauls were converted from grams wet weight of plankton per haul, to grams wet weight per cubic meter of water filtered, assuming 80% filtration efficiency. The derived "Grand Total" maximum wet weight figures for that region north of 45° N. Latitude are, thus computed, about 0.18 g/m³ of water filtered, for the period May to July 1952; conversion to cubic centimeters per cubic meter in a manner similar to treatment of McAllister's (1961) data gives a volume approximately double the average Clarke-Bumpus volume for May 1957, 0.14 cc/m³, the maximum for the year for Washington coastal waters (Fig. 2B). The copepod species making up the bulk of the catch apparently differed widely between the two areas of study; larger calanoids, such as *Calanus plumchrus* and *C. cristatus*, constituted most of the weight of Nakai's western Pacific catch.

For the 0–100 meter level in the same general area of the northwestern Pacific, Bogorov and Vinogradov (1955) show the zooplankton biomass for August to October 1954 ranging from 250 to 500 mg/m³ along a line parallel to the Kurile Islands, and up to 50 miles from their coast. The weights for a band 30 to 50 miles wide farther to the southeast were higher, ranging from 500 to 1000 mg/m³. It was indicated that samples collected in May and June 1953 were larger; although weights did not exceed 500 mg/m³ in the inshore area, they invariably exceeded 1000 mg/m³ in the rich offshore belt. However, the position of the zone of the highest biomass remained the same. Quantity of zooplankton decreased farther to the south and east. The plankton was collected in stratified hauls with Juday nets of No. 38 gauze with an entrance area of 0.1 m² and No. 140 gauze, 0.5 m² entrance area[9]. Even with some allowance for the more shallow (100 m) and possibly richer layer sampled, the comparable coastal waters of the Kurile Islands thus appear somewhat higher in quantity of zooplankton than Washington coastal waters during both periods. A further distinction between the two areas is the difference in species composition; the Bogorov-Vinogradov study, like Nakai's study (1952), reported the common occurrence of large calanoids in the northwestern Pacific.

Plankton investigations carried out as part of the California Cooperative Oceanic Fisheries Investigations (Staff, South Pacific Fishery Investigations 1952, 1953, 1954a, 1954b, 1955, 1956) and Thrailkill (1956, 1957, 1959) in an area of consistent sampling between Point Conception, California and Point San Juanico, Baja, California show monthly average zooplankton displacement

[9]Details of the plankton gear and methods are not listed in the paper, but by personal communications with the office of Dr Bogorov the following information was obtained from Dr C. W. Beklemishev, who was authorized to answer letters in Dr Bogorov's absence. Hauls were vertical using closing Juday nets equipped with a nonfiltering collar whose entrance area of 0.1 m² was smaller than where it attached to the gauze. The biomasses quoted above were obtained from standard hauls. "a) the size of the mesh opening of the No. 38 gauze is 0.185 mm, b) the size of the mesh opening of the No. 140 gauze is about 0.6 mm, c) it is the No. 38 mesh which was used in the standard hauls." Speed of towing was given as approximately 0.6 m/sec; in 1955 no flow meter was used and filtration efficiency was assumed to be 100%. It must be pointed out that the Russian system of mesh openings does not correspond to the Dufour bolting silk scale, i.e., No. 38 above refers to 38 meshes per centimeter rather than to the inch, and furthermore "the numbers of gauze now in use represent the number of strands per centimeter only if the numbers are two-digit. If numbers are three-digit, zero is to be omitted and the two figures which remain represent the number of strands. So No. 38 and No. 140 have 38 and 14 strands per centimeter respectively . . ."

volumes[10] for the period 1951 through 1956 peaking in July at approximately 0.5 cc of zooplankton per cubic meter of water strained for the northern half of the area and a month earlier at approximately 0.34 cc/m³ for the southern half of the area. Except for the year 1951 in the southern half of the area, plankton volumes of less than 0.1 cc/m³ were rarely encountered (Thrailkill, 1959). In contrast in 1957, using the same equipment and tow methods (Silk and Nylon meter nets of 0.65 mm mesh openings, towed obliquely from 140 m depth to surface) a strikingly similar maximum was recorded for the northern area, but in April, decreasing markedly thereafter (Thrailkill, 1959).

A continuation of the monthly survey of the same area during 1958, using identical methods and equipment, showed average zooplankton volumes consistently the lowest recorded in the series of eight years (all less than 0.1 cc/m³) for the period January through November in the northern region off southern California and always less than 0.1 cc/m³ in the more southern region off Baja, California. Although the plankton volumes during 1958 averaged only one-third as large as the 6-year period of 1951–1956, the pattern of abundance was very similar, peaking again in July (Thrailkill, 1961).

In addition to real zooplankton population differences between the present area of investigation and the California coastal area, net size and mesh selectivity, differences of laboratory methods of volume analyses and vertical distribution of organisms in combination with the different depths of towing undoubtedly contribute to volume differences recorded for the two regions. As an example of such variation, based on other information from closing hauls taken off southern California in 1940, Thrailkill (1956) suggests that the average zooplankton volume per unit volume of water in 0–70 meter oblique hauls taken in 1949 and 1950 might be 25% larger than volumes based on hauls from 0–140 meters.

Several studies emphasize that, compared to boreal regions, the central equatorial Pacific has an extremely low zooplankton population; this low population is common to locations in low latitudes, and is most marked in the open ocean. From 210 collections during the period January 1950 to March 1951, King and Demond (1953) report an average wet (displacement) zooplankton volume of 0.027 cc/m³ for the upper 200 m of water for the central Pacific between Latitudes of approximately 27° N to 14° S and Longitudes 155°–175° W. The area of greatest abundance was in the equatorial zone between 6° N and 7° S. Most of the samples were taken with oblique tows of 1-meter nets (0.65-mm mesh openings). It was noted that the mean volume found in the study was about one-tenth the average volume found by the California Cooperative Sardine Research Program (California, Progress Report 1950), which gives a mean zooplankton displacement volume of 0.208 cc/m³ for the whole area along the west coast from 25° N to 47° N for the period April 28 to May 14, 1949. Samples were taken in the upper 70 m of water in oblique tows with similar meter nets.

Later zooplankton sampling in the central equatorial Pacific, during July and August 1952, by Hida and King (1955), covered the area along the 150° W

[10]Volumes used in yearly comparisons are the "smaller" volumes, after removal of organisms whose individual volumes exceeded 5 cc, such as "jellies, fish, squid, salps, pyrosomes . . ."

meridian from 12° N to 7° S latitude. Simultaneous surface, intermediate, and deeper level samplings down to 260 m depth, with Clarke-Bumpus samplers, gave 64.7, 29.2, and 16.6 cc/1000m³, respectively. The Clarke-Bumpus sampler, with its fine-mesh nets (0.31 mm mesh opening) caught more small Copepoda and other small organisms than did the meter net, with its mesh opening of 0.65 mm, in about the same area and season. Although this size selection occurred, the average volumes taken by the two types of gear were about equal. The authors concluded that the loss of smaller organisms in the larger net of coarse mesh was compensated by the inability of the larger organisms to dodge successfully.

In a more recent paper, King and Doty (1957) tabulated zooplankton volumes in the area from 12°25′N. to 7°58′S. and 162°13′W. to 108°37′W. for the period September 26 to December 12, 1955. The average displacement volume of the 115 successful oblique hauls made during the King and Doty study, from an average depth of 231.4 m, was found to be 0.038 cc/m³. Thus the region has a quantity of zooplankton about equal to the average winter minimum volume recorded in Washington waters, but only a quarter of the maximum average volume. Discrepancies between volumes of the catches made in the present study with finer mesh nets (0.239 mm mesh opening) and those made by King and Doty (1957) with coarser mesh nets (0.65 mm mesh opening) will probably not be too great, as indicated by the results of the Hida and King study (1955).

For comparable data on the North Atlantic the reader is referred to a recent study of the volumetric distribution of zooplankton in the Cape Hatteras area by St. John (1958), which includes a table summarizing zooplankton volumes for selected areas to a depth of 200 m.

The values derived in the present study for zooplankton volumes in the upper 200 m of water are considered to be indicative of the population of the area off Washington. Comparison between the samples taken with the quantitative Clarke-Bumpus samplers in oblique tows and those taken by the half-meter net in vertical tows in direct time sequence from the same depth, for each station, shows the same seasonal trend: an increase from a winter minimum to a spring maximum, then through intermediate levels followed by the winter decline. Examination of the few individual pairs of samples which showed the greatest differences in zooplankton volume, with larger volumes in the half-meter net sample, often revealed gelatinous forms which added considerably to the volume of the sample. The quantitative samplers usually took few or none of these forms. Probably the difference in manner of towing was responsible for this type of catch difference; half-meter nets were towed through the water surface, thus sampling gelatinous organisms occasionally present at the surface interface, whereas, the Clarke-Bumpus samplers were always closed just beneath the surface to prevent additional turns of the propeller by wind action, and thus missed some surface organisms. Because the filtration efficiency of the half-meter net is less than 100%, and the water filtered is not directly measured, extremely close comparison of volume of catch by the two types of gear is unwarranted.

Consistent comparison of these paired tows facilitated the elimination from the study of nonquantitative or non comparable samples (such as those vitiated by inadvertent use of a net of different mesh on the quantitative sampler, field error in reading the counting mechanism, or improper technique resulting in malfunction of gear).

Thus the figures found in this study, for the zooplankton volumes in the Washington coastal area, are considered sufficiently accurate to admit of valid comparison with figures for the northwestern Pacific in areas of similar latitudes and proximity to coastline; the volume in the Washington area was less, and the major species composition was different. In sharp contrast to the northern areas is the central equatorial Pacific, which yielded volumes ranging, during the year, from 0.027 cc/m^3 (King and Demond 1953) to 0.038 cc/m^3 (King and Doty 1957). These figures approximate the average winter minimum figure for Washington coastal waters, but they are only one-fourth to one-fifth of the average maximum displacement volume recorded in May.

Anomalous Water Intrusion

Chemical and physical data for the 6 cruises are shown in Fig. 2. The average temperatures for February 1958 exceeded those of February 1957 by 2.36° at the surface level and by 0.71° at the 200-meter level.

Further corroboration of anomalous conditions is given by a comparison of surface temperatures during 1957–58 with the 20-year mean average for January and February for Neah Bay, Washington, by Stewart, Zetler and Taylor (1958). They show an anomaly of 2.9°F (1.6°C) in January, 1958, peaking at 4.4°F (2.4°C) in February of 1958, with similar anomalies at 10 stations sampled from La Jolla, California, to Sitka, Alaska. As described by the authors these anomalies cannot be considered seasonal variations but appear to be due to a diminution or termination of the usual upwelling conditions along the coast and an onshore movement of water caused by a change of measured wind conditions. A large rise in sea level was also noted.

For the months of February, the difference in average amount of dissolved inorganic phosphate at the surface also was great. In February 1957, all stations, with one exception (0.97 μg-at/liter), yielded more than 1.0 μg-at/liter, averaging 1.22 μg-at/liter. In February 1958 all stations yielded *less* than 1.0 μg-at/liter, averaging 0.82 μg-at/liter: the average decrease was thus more than 30% (Fig. 2). At the 200-meter level also, the average amount of phosphate was somewhat smaller in February 1958.

Fleming (1955) in figure 14, shows surface phosphate values of 1.0 μg-at/liter between the Washington coast and 125°W. The concentrations decreased toward the southwest with a value of only 0.5 μg-at/liter within 200 miles of the coast. Although Fleming's values are for the summer, the surface values reported here for February 1957 are similar, in fact on the average 20% higher. In February 1958, on the other hand, a conspicuous reduction was noted in this coastal region. This would be expected if there were a northeasterly movement of the surface water (assuming, of course, a winter gradient in the same direction

as the summer gradient). Additional strong evidence for such a flow has been given by Dodimead and Hollister (1958) and Tully *et al.*, (1960) who described drift bottle recoveries and anomalous temperature conditions respectively.

It may be noted that the average Clarke-Bumpus zooplankton volume for the sampling area of the present study during February 1957 (0.091 cc/m^3), was more than 3 times as large as in February 1958 (Fig. 2, B). The inshore and offshore average zooplankton volumes for February 1957 were in a ratio of about 2 to 1 (0.134 to 0.065 cc/m^3); however, in February 1958, the volumes were similar to each other and much lower (0.029 and 0.024 cc/m^3).

The "normal" zooplankton population that might have been expected, on the basis of 1957 data, in the upper 200-meter layer in February 1958, apparently was replaced by the intrusion of a warmer water mass carrying with it its endemic population.

Acartia danae Distribution

The periodic or occasional appearance of the copepod species *Acartia danae* in Washington coastal waters may be closely connected to the general oceanic circulation of this coastal area.

In samples collected by the Albatross expedition (Wilson, 1950), the species was taken at a number of stations between California and Hawaii, and at others in the area around the Phillippine Islands and Formosa; the species was also listed as taken in the Bering Sea[11].

Samples from the Carnegie collections (Wilson, 1942), showed *A. danae* to be widely distributed in the Pacific. The species was notably missing, however, from two sections of the cruise tract; one was in the eastern South Pacific, the other in the arc of stations from Japan to northern California north of 40°N Latitude, taken in July. All these Carnegie tows were made in the upper 100 m of water.

In the areas where *A. danae* was present, its common occurrence in both day and night hauls indicated indifference to ordinary light (Wilson, 1942). Johnson (1942) lists the species as one not previously found in the area just off the California coast (31°–35°N Latitude); his tows usually were from the upper 200 m of water.

Mori (1937) recorded the presence of *A. danae* only in several samples taken during August in different years just off the Japanese coast in the upper 100 m of water. For the northwestern Pacific, Bogorov (1958) lists *A. danae* as found in surface layers down to 200 m in tropical waters of 18° to 27° temperature, as well as in an intermediate zone of mixing with temperatures from 15° to 18°. However, unlike Wilson (1950) he does not list the species farther north in boreal waters; the zone of mixing extended to approximately 40–45°N Latitude at its northern boundary, in the area from the Japanese coast eastward to 170°E.

[11]The presence of *A. danae* in the Bering Sea is a notable exception to the warmer and more southern water distribution noted by other researchers (Johnson, 1942; Bogorov, 1958); the material should be re-examined, as Bogorov (1958) notes that some of Wilson's identifications are not reliable.

No record of the species has been found in any of the literature dealing with the British Columbia coast nor has the species been noted in preliminary examinations of samples taken in the Gulf of Alaska.

In December 1956, the presence of *A. danae* was noted by the author in a single sample (Station 151–14) taken in the southwestern part of the 151 cruise track (Figure 1). In February 1957 the species was observed in a line of six stations forming a crescent opening to the south (Fig. 1). During May, only a single female specimen was captured. No specimens were observed on the later cruises of July and November 1957. In February 1958 the species reappeared at three stations. Previously, this species had been noted by Davis (1949) and Wilson (1950). Davis recorded *A. danae* in September 1935, in one sample taken in the top 10 meters of water, on the southern edge of the present area of study. Wilson lists the species as taken "off Washington" in November 1905, during the Albatross expedition; the actual location listed was well inside Puget Sound near Seattle (No evidence of the presence of *A. danae* in the Seattle area of Puget Sound was noted in a weekly program conducted by Hebard (MS, 1956) while simultaneously sampling other species of *Acartia* at two depths, 0–57 and 57–148 m, over a period of a year).

Except for station 158–19 (taken off the entrance to Gray's Harbor, Washington, in February 1957), all stations at which *Acartia danae* were recorded in the present study had salinities ranging from 32.24‰ to 33.96‰; temperatures from 6.16° to 12.66°, for the 200-meter layer of water sampled. For station 158–19, both temperature and salinity increased down to 71 m; salinity of 32.14‰ and temperature of 7.75° were recorded at 30 m.

In August 1956, larger numbers of *A. danae* (29/m^3) were taken in the upper 200 meters of water at station 144–25 (40°01′ N, 127°34′ W), where the salinity from surface to 200 m ranged from 32.80‰ to 33.88‰; the temperatures from 16.31° to 6.81°, respectively. No specimens were taken on this station in a simultaneous haul on the same cable from 400 to 200 meters depth, nor in any other haul below 200 m at other stations of this southern-ranging cruise. During this same cruise, on August 21, 1956, *A. danae* was taken at station 40, at 46° north latitude off the Washington coast, south of the present area of study, but not at any of the other stations of cruise 144 in the present area of study or north of it[12].

Thus for all stations for which *A. danae* were recorded, salinities of more than 32‰ were common and temperatures ranged from 6.16° to 16.31°. The species was most abundant in water of higher temperatures. The specific range of salinity and temperature within which the organism is common, however, may be much narrower than the limits described, as precise depth of capture was not determined.

In regard to the Washington coast, *Acartia danae* appears to have been carried into the area from a location farther south during February, particularly in 1957. Fleming (1955) has indicated the presence of the northerly flow of the

[12]See insert, Fig. 1, for station locations. For locations for other stations of the latter cruise, see Love, 1957.

Davidson Current along the western coast of North America during the winter only; in the summer a southerly flow is indicated. In the summer period, from July through November 1957, no *A. danae* were recorded in the Washington coastal area. The above data indicate that the species thrives in warmer waters and is most common in surface zones. The circumstances of the appearances of *A. danae* along the Washington coast suggest that the species is carried into the area seasonally by the prevailing circulation but has not established itself as a permanent resident. The presence of the species at a single station in December 1956 (Fig. 1) might be indicative of the beginning of the seasonal arrival of the species from an area farther south; whereas the single female specimen in May 1957 might be a straggler from the previous winter season. Temperature is possibly a controlling factor. The geographic extent and periodic variation of *A. danae*, correlated with oceanographic conditions, suggest its possible use as a species indicative of water of a more southerly origin off the Washington coast.

SUMMARY

1. Zooplankton samples were dominated by the copepod species *Pseudocalanus minutus* and *Oithona similis*.

2. A regular temporal progression of zooplankton volumes over an annual cycle is evident in the upper 200 meters of Washington coastal waters. The minimum average displacement volumes for oblique hauls of Clarke-Bumpus samplers (0.239 mm mesh nets) were 0.035 and 0.025 cc/m^3, in December 1956 and February 1958, respectively. The maximum average displacement volume for the area was 0.139 cc/m^3, recorded during the middle of May.

3. Average zooplankton volumes taken with vertical tows of half-meter nets of the same mesh, from 200 meters to the surface, also showed a regular seasonal progression of abundance, and agreed closely in time and abundance with the quantitative sampler results.

4. Higher zooplankton volumes were usually recorded nearer the coast: for the period December 1956 through November 1957 the limited data available showed average volumes for the areas inside and outside the 100-fathom contour line to be respectively, 0.147 cc/m^3 and 0.075 cc/m^3.

5. Volumes of zooplankton recorded in Washington coastal waters were similar to those reported in the Gulf of Alaska but less than those waters of the northwestern Pacific which are similar in latitude and proximity to coastline; in major species composition, the northeastern and northwestern areas differed widely. Reported zooplankton volumes off the California coast were higher for the period 1951–1957, but lower in 1958 in comparison with the results of the present study. Although the winter minimum volume recorded for the Washington coast resembles those reported for the central equatorial Pacific throughout the year, the Washington spring maximum is four to five times the equatorial standing crop.

6. For the area of this study, lower zooplankton volumes, accompanied by change of species composition, were recorded in February 1958 than in February

1957. This change accompanied an increase of 2.36°C in surface temperature and decrease of 30% in amount of dissolved inorganic phosphate, which occurred in 1958. The data given in conjunction with supporting concurrent oceanographic and meteorological records taken by other authors show that February 1958 had an unusual fluctuation: water from regions farther offshore appeared to replace the "normal" water with its zooplankton population.

7. The periodic occurrence of the copepod species *Acartia danae* during the winter months and its disappearance during the summer, in conjunction with the described north-south seasonal alternation of coastal water flow, suggests the possible use of this organism as a species indicative of water of a more southerly origin.

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Decapod Crustacea of the *Calanus* Expeditions in Frobisher Bay, Baffin Island, 1951[1]

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ABSTRACT

About 600 specimens of decapods comprising 11 species were collected by trawl and dredge on the Calanus Shelf and by plankton net at Potter Island by the *Calanus* expeditions in 1951.

Stations at the shallower parts of the shelf yielded the greater number of specimens of decapods, those on the outer slope of the shelf fewer decapods but more echinoderms, and a station deeper and shoreward from the shelf in Victoria Bay no decapods at all.

Specimens were mostly of the family Hippolytidae, and were dominated in numbers by *Lebbeus groenlandicus*. Their size distribution was similar to those from Ungava Bay but maturity was apparently later and at a somewhat larger size. Most species appeared to spawn annually as shown by percentage of mature individuals carrying eggs or ready to spawn in autumn.

The decapod fauna on the Calanus Shelf was similar to that of the shallow water areas of Ungava Bay, but lacked species which might show any influence of Atlantic water incursions.

Stomach contents evinced feeding on benthos on the shelf, almost all having some fine sand and phytobenthos. A greenish ostracod, large *Elphidium*-like foraminiferans visible to the unaided eye, and polychaete setae occurred in stomachs quite frequently.

INTRODUCTION

As far as the present author is aware no collection of decapod Crustacea had been made in Frobisher Bay prior to that by the *Calanus* expeditions in 1951. Grainger (1953) reported some decapod larvae in stomachs of arctic char taken in Frobisher Bay in 1948, 1950 and 1951.

Dunbar (1958) has described the physical oceanographic and geographical features of the bay. It has a deep trough of over 600 metres to the southwest. Rather extensive areas less than 100 m deep occur at the head of the bay, in its northeast portions, and on the "Calanus Shelf" situated on the east side near the entrance (Dunbar, fig. 5).

The location of the stations in Table I is shown on page 104 of Grainger (1954). Most of the collections reported here were made on the Calanus Shelf. Stations 317, 318, 331 and 406 were at depths less than 100 m on the shelf, while stations 322, 333 and 334 were deeper than 100 m, just at the western edge of the shelf. Decapods were also taken by dredge on the southeastern edge of the shelf at two of the series of stations crossing the mouth of the bay (319, 321) in depths of 115 and 70 m. Plankton hauls obtained decapods at station 310 in a

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TABLE I. Decapod crustacean species composition of the Calanus Shelf (Frobisher Bay) fauna as taken by dredge and beam trawl by the *Calanus* expeditions in 1951. The plankton net haul was made at Potter Island (set 310) on the south side of the bay near the entrance. Echinoderm species (total specimens) from Grainger (1955).

Station	310	317	318	319	321	322	331	333	334	406			
Depth, *metres*	14–27	27–36	55	113–118	71	119	77	104–137	183–192	46			
Type of gear	Pl. net	Dredge	Dredge trawl	Dredge	Dredge	Dredge trawl	Trawl	Trawl	Trawl	Dredge	Av. carapace length		
Length of tow, *min.*		10-	9	10	15	13	8	45	20	5	Male	Female	Total
											mm		
Eualus fabricii	17	10	7	..	..	1	3	..	..	5	6	10	43
E. gaimardi belcheri	..	..	..	..	..	..	..	..	1	..	11	..	1
Spirontocaris lilljeborgi	..	..	..	1	..	..	..	..	..	..	11	..	1
S. phippsi	33	4	5	1	2	..	..	..	..	..	5	7	45
S. spinus	..	..	2	4	..	53	2	2	2	2	9	11	67
Lebbeus groenlandicus	..	2	114	..	6	..	37	1	..	35	12	16	195
L. polaris	69	5	30	..	..	3	2	1	2	10	9	13	122
Sabinea septemcarinata	..	..	..	..	..	4	..	..	..	..	11	17	4
Argis dentata	4	..	4	..	..	31	5	1	13	..	13	17	58
Sclerocrangon boreas	..	1	11	..	..	1	3	1	..	2	17	21	19
Pagurus krøyeri	..	14	6	4	1	1	9	3	1	12	14	10	51
Total	123	36	179	10	9	94	61	9	19	66	..	..	606
Crinoidea	..	..	..	1	..	1	1	1	2	..	..	..	..
Asteroidea	..	6	3	11	3	..	..	..	1	6	..	..	..
Ophiuroidea	..	32	6	52	5	..	3	15	3	13	..	..	..
Echinoidea	..	..	1	6	..	2	..	7	7	5	..	..	..
Holothuroidea	..	2	..	..	..	..	..	..	..	2	..	..	..

small inlet of Potter Island, at the entrance of the bay on the southwest side, over an approximate depth of 25 m.

The hydrography of the area at the time of collecting (Fig. 1; Dunbar, 1958) indicates that bottom water at stations 322, 331, 333, 334 and 406 (Table I) was at a temperature of about −1.0°C; at stations 319 and 321 just below 0°C; and at stations 317 and 318 just above 0°C. Stations 319 and 321, at the easterly edge

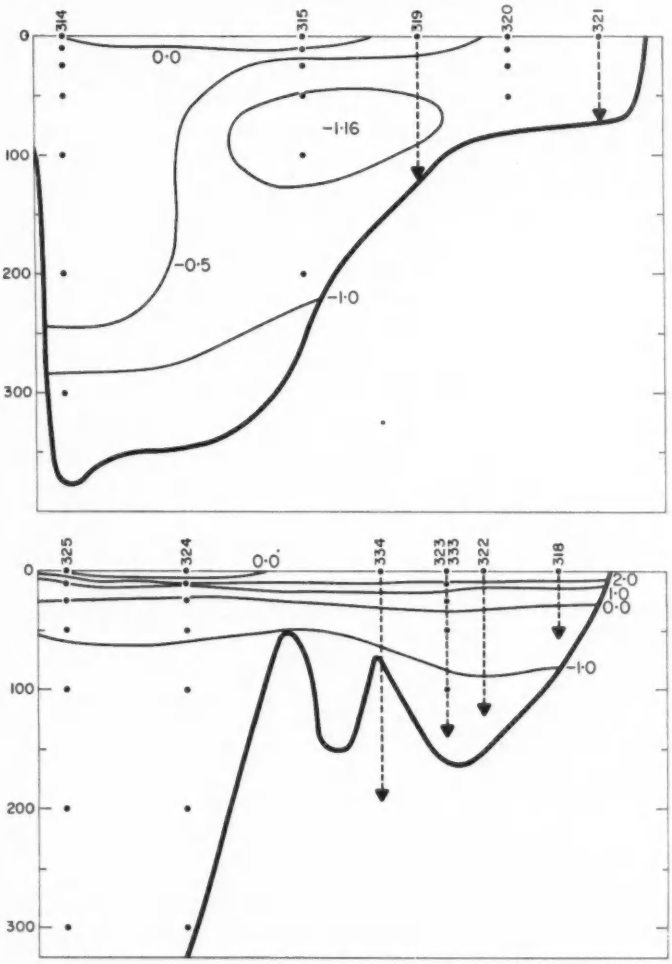

FIG. 1. Two hydrographic sections on the Calanus Shelf in 1951, from figure 13 of Dunbar (1958), with 6 trawling stations where decapod Crustacea were taken indicated by arrows. *Above:* Section VII, across the bay a few miles inside the mouth. *Below:* Section VIII, across the bay about 37 nautical miles inside Section VII (Dunbar, fig. 2). Depths in metres; isotherms in degrees Centigrade.

of the Calanus Shelf near the entrance to the bay, were shallower than the sill at its mouth (300 m, Dunbar, 1958).

Specimens were taken by beam trawl and dredge on the Calanus Shelf and by plankton net at Potter Island (Table I). Methods of treatment were similar to those used elsewhere in this series (Squires, 1957).

SYNOPSIS OF THE SPECIES COLLECTED

Family **Hippolytidae**

Eualus fabricii (Krøyer, 1841)

These were taken at 5 stations (Table I), all on the Calanus Shelf at depths of 27–119 m. The greatest number of specimens (17) were taken at Potter Island in a plankton net from a depth of about 25 m; these were mostly juveniles or small adults 4–6 mm in carapace length. Since no strictly benthonic decapod (e.g. *Pagurus*) was taken in set 310 it would appear that these juveniles and small adults of *E. fabricii* were, to some extent at least, pelagic.

In these collections the smallest mature specimens of this species had a carapace length of 9 mm in both males and females (Table II), while in Ungava Bay the males were first mature at 6 mm and the females at 8 mm (Squires, 1957). Average carapace length of specimens from the Calanus Shelf was 10 mm in females (range 4–12 mm; 31 specimens; Fig. 2).

TABLE II. Maturity of decapod crustacean species in August, 1951, on the Calanus Shelf, Frobisher Bay, taken by the *Calanus* expeditions. Numbers in parentheses are possibly mature but with small eggs.

	Males				Females					
Species	Juvenile	Vas deferens small	Vas deferens large	Carapace length 1st mature	Not ovig. small eggs	Not ovig. large eggs	Ovigerous	Carapace length 1st ovig.	Mature; spawning in autumn	Carapace length 1st mature
				mm				*mm*	%	*mm*
Eualus fabricii	..	..	1	9	13 (11)	0	12	9	52	9
E. gaimardi belcheri	..	1	..	..	..	..	..	..	..	..
Spirontocaris lilljeborgi	..	..	1	11	..	..	..	..	..	..
S. phippsi	..	1	3	..	4 (3)	5	3	6	73	6
S. spinus	..	23	2	10	23 (13)	13	4	13	57	10
Lebbeus groenlandicus	9	31	30	12	67 (34)	42	12	16	61	14
L. polaris	1	8	11	11	9 (5)	6	5	12	69	11
Sabinea septemcarinata	..	1	..	..	..	2	1	17	..	14
Argis dentata	2	21	8	13	18 (3)	4	3	22	70	20
Sclerocrangon boreas	..	1	2	15	7 (1)	4	2	27	86	24
Pagurus krøyeri	11	7	15	11	15 (0)	5	1	16	100	11

About 90% of the females caught were mature and 50% of the mature females were ovigerous in August. No mature females had large ready-to-lay eggs in the ovaries (Table II). Therefore, a spawning of individuals only once in two years is indicated (Squires, MS).

Eualus gaimardi belcheri (Bell, 1855)

Only one immature male was taken, 11 mm in carapace length, at station 334 (Table I).

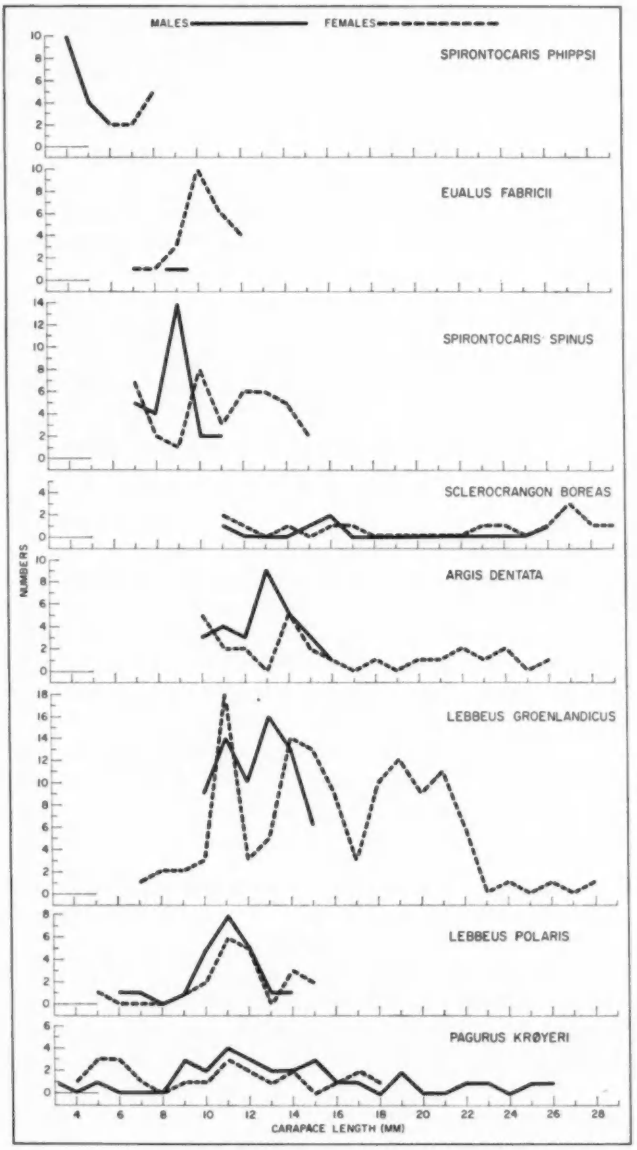

FIG. 2. Frequency of male and female decapod Crustacea at various carapace lengths taken on the Calanus Shelf, Frobisher Bay, 1951.

Spirontocaris lilljeborgi (Danielssen, 1859)

Only one mature male was taken, 11 mm in carapace length, at station 319 (Table I).

Spirontocaris phippsi (Krøyer, 1841)

Nine specimens were taken on the Calanus Shelf (stations 317, 318) and 3 near the mouth of the bay (stations 319, 321). At Potter Island 33 specimens were taken in a plankton net which touched bottom. Since a large proportion of those taken in the plankton net were juveniles or small adults 3–7 mm in carapace length, it may be presumed that at this size they are at least occasionally pelagic in habit.

Average carapace length of those taken on the Calanus Shelf in males was 5 mm (range 4–6 mm; 16 specimens) and in females 7 mm (range 5–8 mm; 15 specimens; Fig. 2). Females were first mature (ovigerous) at 6 mm and males at 5 mm in length (Table II) compared with 6 and 4 mm, respectively, in Ungava Bay specimens (Squires, 1957).

About 75% (total 11 mature specimens) were either ovigerous or with large eggs in ovaries in August suggesting annual spawning in the mature individuals in this population.

Spirontocaris spinus (Sowerby, 1805)

This species appeared in 6 stations on the Calanus Shelf, and one at the mouth of the bay (Table I). Average length of carapace in males was 9 mm (range 7–11 mm; 27 specimens) and 11 mm in females (range 8–15 mm; 40 specimens; Fig. 2). Males and females were first mature at 10 mm in carapace length (Table II) about 3 mm larger than when first mature in Ungava Bay specimens (Squires, 1957).

About 55% of the mature females in August would spawn during the autumn (Table II). This low percentage would suggest spawning of individuals in alternate years in this area.

Lebbeus groenlandicus (J. C. Fabricius, 1775)

This species was numerically the dominant decapod on the Calanus Shelf (Table I). Average carapace length in males was 12 mm (range 10–15 mm; 68 specimens) and in females 16 mm (range 7–28 mm; 124 specimens; Fig. 2). Males were first mature at 12 mm and females at 14 mm carapace length (Table II; 10 and 14 mm, respectively, in Ungava Bay specimens; Squires, 1957).

About 60% of the females were ovigerous in August or would spawn during the autumn indicating biennial spawning by individuals in this population (Table II).

Lebbeus polaris (Sabine, 1821)

This species was second in abundance to *L. groenlandicus*. It occurred in greatest numbers in the oblique plankton haul at Potter Island (Table I). On the Calanus Shelf carapace lengths averaged 9 mm in males (range 6–14 mm; 23 specimens) and in females 13 mm (range 5–15 mm; 20 specimens; Fig. 2).

In set 310 at Potter Island they were smaller: males 4–10 mm and females 5–12 mm (Fig. 3), while a fair number (23) were juveniles at 3 mm, being presumably more pelagic at the smaller sizes.

Males and females were first mature at 11 mm (Table II), as compared with first maturity at 8 mm (♂) and 10 mm (♀) in Ungava Bay specimens (Squires, 1957). About 70% of the females were ovigerous or would be ovigerous in autumn, indicating probable annual spawning (Table II).

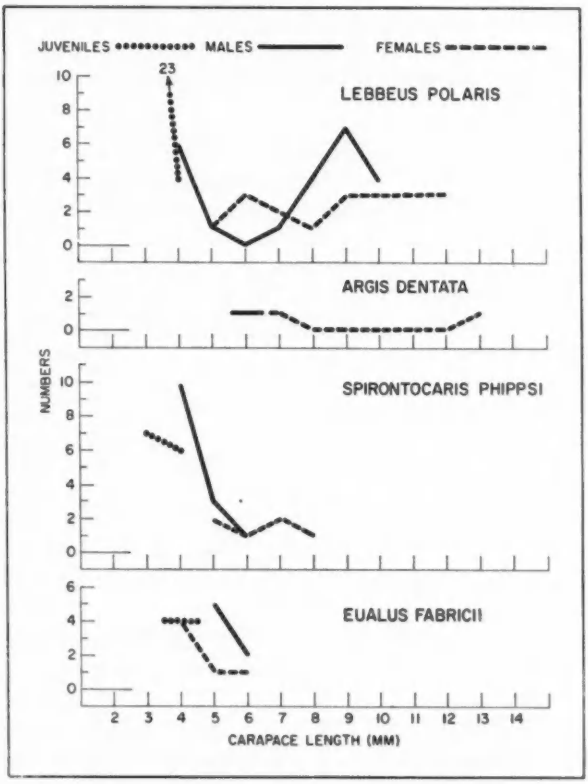

FIG. 3. Frequency of male and female decapod Crustacea at various carapace lengths taken in plankton net at Potter Island, Frobisher Bay, 1951.

Family **Crangonidae**

Sabinea septemcarinata (Sabine, 1924)

Four specimens only were taken on the inner slope of the Calanus Shelf (Table I). These were: 1 immature male, 11 mm carapace length; 3 mature females, 14–19 mm, one of which was ovigerous at 17 mm.

Argis dentata Rathbun, 1902

This species appeared in catches from 5 stations on the Calanus Shelf (Table I), and some were taken in the plankton net at Potter Island. Since this species has modified pereiopods for swimming it would be expected to have at least a partly pelagic existence.

Average carapace length in males was 13 mm (range 6–16 mm, 28 specimens) and in females 17 mm (range 6–26 mm, 26 specimens) (Fig. 2). Males were first mature at 13 mm and females at 20 mm in length (Table II), as compared with 9 and 16 mm in Ungava Bay (Squires, 1957).

Seventy per cent of the mature females would be ovigerous in autumn. This would suggest annual spawning, although the sample was small (10 mature).

Sclerocrangon boreas (Phipps, 1774)

This species was taken in small numbers at 6 stations on the Calanus Shelf (Table I). The specimens varied from the characteristic long-spined type (centre dorsal spine doubled) similar to specimens from Ungava Bay (Squires, 1957), to the short-spined type described in Rathbun (1929).

Average carapace length in males was 17 mm (range 11–16 mm, 5 specimens) and in females 21 mm (range 11–29 mm, 14 specimens; Fig. 2). Males were first mature at 15 mm and females at 24 mm (Table II): males at 9 mm (1) in Ungava Bay specimens (Squires, 1957).

About 85% of those mature would spawn in autumn (Table II), suggesting annual spawning of this species on the Calanus Shelf.

Family **Paguridae**

Pagurus kröyeri Stimpson, 1857

Small numbers of this species were taken at all bottom stations in the bay (Table I). Average carapace length was 5 mm (range 3–8 mm) in juveniles (10 specimens), 14 mm in males (range 5–26 mm; 29 specimens) and 10 mm in females (range 4–18 mm; 22 specimens) Fig. 2.

All mature specimens would spawn in autumn (Table II), suggesting annual spawning in this area.

Stomach Contents

Greenish phytobenthos was present in almost all decapod stomachs from all sets on the Calanus Shelf. Centric and some pennate diatoms, with occasional filamentous algae, contributed most to its bulk. Fine sand was present quite frequently. Two large *Elphidium*-like species of foraminiferans occurred quite often in considerable numbers, with occasional *Discorbis* and *Hormosina* (all visible to the unaided eye). A greenish ostracod with a delicately sculptured shell was present, while polychaete setae were seen quite frequently as well as other polychaete remains. Probably parts of burrowing forms were cropped off. Fragments of crustaceans were only rarely seen; these included euphausiids, shrimp and cumacean remains in stomachs of the larger species: *L. groenlandicus*, *Sclerocrangon boreas* and *Argis dentata*. Small quantities of hydroids and alcyonarians were found infrequently.

TABLE III. Stomach contents of decapod Crustacea of the Calanus Shelf and Potter Island, Frobisher Bay.

Stomach contents	Calanus Shelf												Potter Island					
	Eualus fabricii	*E. gaimardi belcheri*	*Spirontocaris liljeborgi*	*Spirontocaris phippsi*	*Spirontocaris spinus*	*Lebbeus groenlandicus*	*Lebbeus polaris*	*Sabinea septemcarinata*	*Argis dentata*	*Sclerocrangon boreas*	*Pagurus kroyeri*	Total	*Eualus fabricii*	*Eualus gaimardi belcheri*	*Spirontocaris phippsi*	*Lebbeus polaris*	*Argis dentata*	Total
Phytobenthos	12	1	1	5	16	84	19	2	12	10	24	186	2	..	3	13	..	18
Ostracod	1	..	..	3	5	40	7	..	..	..	4	60	..	..	..	2	..	2
Polychaetes	3	..	..	..	..	41	8	..	5	8	6	71	..	..	1	..	..	1
Foraminifera	3	..	1	3	14	17	7	..	1	1	18	65	..	..	1	..	..	1
Amphipods	..	..	..	..	..	7	1	..	4	1	1	14	..	..	..	..	..	..
Hydroids	2	..	..	..	1	6	4	..	1	1	4	19	..	..	1	2	..	3
Small pelycopods	..	..	..	..	2	..	..	..	4	..	..	6	..	..	..	..	..	..
Alcyonaria	..	..	..	..	..	2	..	..	..	..	..	2	..	..	..	..	..	..
Gastropods	..	..	..	..	1	3	..	..	3	1	..	8	..	..	..	..	..	..
Euphausiids	..	..	..	..	..	3	..	..	..	5	..	8	..	1	..	..	..	1
Shrimp fragments	..	..	..	..	..	1	..	..	..	..	..	1	..	..	..	..	..	..
Cumacea	..	..	..	..	..	..	..	..	1	..	..	1	..	..	..	..	..	..
Sand	11	1	1	3	16	78	20	3	11	11	26	181	3	..	4	12	..	19
Total stomachs examined	19	1	1	4	20	97	28	4	29	18	37	258	3	1	4	20	..	28

DISCUSSION

"The Calanus Shelf offers excellent trawling bottoms consisting of sandy mud with shells and fine gravel, but the fauna itself is not rich" (Dunbar, 1958). Since, in spite of the number of decapods taken in 10 sets, this collection is in bottles occupying only 1.3 cubic feet of storage space, it must be conceded that the decapod fauna does not bulk large in the area. However, members of the family Hippolytidae, which comprised most of the species and specimens present, are small individually and do not produce a heavy crop anywhere in the northwest Atlantic. The frequent occurrence of their larvae in stomachs of arctic char (Grainger, 1953) suggests a higher degree of productivity than the actual volume of specimens would indicate.

The decapod fauna of the shelf: *Lebbeus groenlandicus*, *L. polaris*, *Spirontocaris spinus*, *S. phippsi*, *Eualus fabricii*, *Argis dentata* and *Sclerocrangon boreas* was similar to that of the shallow water areas of Ungava Bay (Squires, 1957).

Temperature did not appear to appreciably affect the distribution of decapods in Frobisher Bay. There was a tendency for greater depths to have smaller numbers and fewer species, but depths over 200 m were not fished. Table I includes a summary of the echinoderms taken in the hauls which had decapods. There is some tendency for echinoderms to replace decapods in the deeper hauls on the outer edge of the Calanus Shelf (No. 319, 333, 334), though not at the one fairly deep haul on the shelf proper (No. 322). Grainger (1954, 1955, and personal communication) reports that in set 329 in Victoria Bay, on the shoreward side of the shelf at 183 m, a "fairly large haul" was taken which included 34 specimens

of ophiurans (mostly *Ophiocten*), 12 sea cucumbers (*Myriotrochus*), a few polychaetes and some specimens of the bivalves *Nucula belotti* and *Macoma calcarea*, but no decapods.

Hydrographic evidence shows a considerable difference between Ungava and Frobisher Bays, particularly a near absence of Atlantic influence in the latter (Dunbar, 1958). Consistent with this is the lateness of maturity in several Frobisher Bay decapods, notably *Eualus fabricii*, *Spirontocaris spinus*, *Lebbeus polaris* and *Argis dentata*, as compared with the same species in Ungava Bay. Also, the number of species is smaller; while this may in part be related to the smaller number of specimens in the collection, significant absentees are *Pandalus montagui* and *Eualus macilentus* which may be considered low arctic species in the western Atlantic. *Pasiphaea* and *Sergestes* could not be expected at all unless there were an Atlantic water influence, and then only if greater depths had been fished (Squires, 1957).

The decapod fauna of Frobisher Bay, like that of Ungava Bay, has a resemblance to the decapod fauna of west Greenland although lacking some important species (Squires, 1957). The origin of this fauna in a colonization process could be from the east as well as the south, since west Greenland currents in the north add to the great volume of arctic water flowing from Lancaster Sound down along the east coast of Baffin Island (Dunbar, 1951). At the present day Atlantic water would undoubtedly bring faunal elements from west Greenland to Ungava Bay, but perhaps rarely to Frobisher Bay. The southeasterly direction of the opening of the latter bay, and its lack of a deep channel at the entrance (Dunbar, 1958), put it in a much less favourable position than Ungava Bay to receive Atlantic incursions.

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MS. Shrimps (Penaeidea and Caridea) collected in Newfoundland and Labrador, 1946–1957. In preparation.

Distinctions Between the Broad Whitefish, *Coregonus nasus*, and Other North American Whitefishes[1]

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ABSTRACT

176 specimens of *C. nasus* and 121 of "humpback" whitefish (allied to *C. clupeaformis*) were examined from 15 North American localities where the two kinds occurred sympatrically. No previously published criteria were effective in separating the two kinds at all sizes in all localities, but combinations of certain pairs of measurements chosen to compensate for non-isometric growth allowed identification of all individuals examined. Length of longest gill raker was less than 20% of the interorbital width in all *C. nasus*, more in all "humpbacks". Means of 15 other proportional or meristic characters differed consistently between sympatric species pairs. *C. nasus* is a distinct and widespread species. Its distribution and nomenclature are reviewed.

INTRODUCTION

Whitefishes are notoriously difficult to classify. Their characters are readily modified by the environment, so that species from one body of water cannot easily be equated with those from another. Taxonomic confusion has resulted. The 40 North American whitefish species in Jordan, Evermann and Clark's checklist (1930) are lumped as only 21 species in the recent American Fisheries Society list (Bailey, 1960). In Eurasia, of 13 *Coregonus* species recognized either by Berg (1948) or Svärdson (1957), only 4 are common to the two authors. Attempts to correlate North American with Eurasian species have been correspondingly confusing. For example, the widespread North American lake whitefish *C. clupeaformis* has been tentatively equated to three different Eurasian species by three different recent authors (Walters, 1955; Svärdson, 1957; Gasowska, 1960).

The present contribution attempts only to show that, within this complex, one species *Coregonus nasus* stands distinct from all others in North America. This is by no means a new opinion (e.g. Walters, 1955), but it has been challenged by Dymond (1943), and more recently by Svärdson (1957), each of whom suggests that *C. nasus* is not different from *C. clupeaformis*.

This study is presented firstly because new material from northern Canada and Alaska has become available, and secondly because I believe that clarification can be achieved by concentrating on localities where two related species live sympatrically. Examination of many specimens from each such locality can reveal whether the species there are in fact distinct. It can also indicate the

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best characters to distinguish between the species over a wide size range. After a number of such sympatric pairs have been studied, the task of equating species from different localities can be attempted with better knowledge of the limitations of the characters used. In this paper, with emphasis on collections of sympatric pairs and on the changes in body proportions which accompany growth, the conventional "key characters" for identification of *C. nasus* are re-examined and improved.

TABLE I. Localities from which whitefish species pairs examined.
C: *Coregonus nasus;* H: "humpback" whitefish.
BC: University of British Columbia; ROM: Royal Ontario Museum;
SU: Stanford University.

Map No.	Locality	Lat. N, Long. W	Museum No.	*No. of specimens* C	H
	Kuskokwim River				
1	McGrath	62°58′, 155°38′	BC60–359	0	2
			BC60–361	4	0
	Yukon River System				
2	Alakanuk	62°40′, 164°36′	BC60–386	2	8
			BC60–387	2	2
3	Between Andreafsky and Kwiguk	62°20′, 163°50′	SU 19022	1	0
			SU 13879	0	1
4	Andreafsky (St. Marys)	62°03′, 163°10′	BC60–391	12	12
			BC60–393	2	0
5	Near Dawson City	64°04′, 139°25′	ROM 5681	1	0
			ROM 5689, 5691	0	2
6	Lake Laberge	61°11′, 135°12′	BC57–223	1	6
7	Teslin Lake	60°15′, 132°57′	BC53–165A	5	5
			BC58–295	0	6
			W. A. Clemens	12	12
	Colville River				
8	Ocean Point	70°10′, 150°55′	BC58–559	1	0
			BC58–561	2	1
	Mackenzie River				
9	Peel R., S. of Aklavik	68°12′, 135°00′	ROM 10898	1	0
			ROM 10854, 10855, 10892, 10893, 10894, 10897, 10899, 10900, 10903.	0	9
10	Kittigazuit	69°21′, 133°41′	ROM 10261, 10262, 10526, 10527, 10528, 10530	6	0
			ROM 10263, 10264 10529, 10531, 10532.	0	5
11	Tuktoyaktuk	69°27′, 133°02′	J. G. Hunter	12	11
12	**Anderson River**	69°45′, 129°00′	J. G. Hunter	91	23
	Coppermine River System				
13	Coppermine village	67°50′, 115°05′	BC59–456	0	1
			BC59–462	0	1
			BC59–463	1	0
14	Dismal Lakes	67°26′, 117°07′	UBC and ROM	14	15
15	Redrock Lake	65°28′, 114°10′	UBC and ROM	7	8

MATERIAL

Most specimens examined are in the museum of the Institute of Fisheries at the University of British Columbia. Additional collections were studied at Stanford University and the Royal Ontario Museum, and data were supplied by Dr W. A. Clemens on some Teslin Lake fish and by Mr J. G. Hunter on specimens from Tuktoyaktuk and Anderson River. Table I and Fig. 1 show localities from which specimens of *C. nasus* and sympatric "humpback" whitefish (as defined later) were available. Specimens from Dismal and Redrock Lakes were obtained during the 1959 survey of the Barren Grounds by the Arctic Unit of the Fisheries Research Board of Canada, and will eventually be deposited some in the Royal Ontario Museum and some at the University of British Columbia. Also examined briefly by the author but not included in Table I were 1 specimen of *C. nasus* from Herschel Island, and 1 of *C. nasus* and 3 of "humpback" from King Point on Mackenzie Bay, all taken by the Arctic Unit of the Fisheries Research Board of Canada.

The size range of these specimens may be seen in Fig. 5 and 6. The greatest range covered by any one collection was from Andreafsky, with standard lengths of *C. nasus* ranging from 188 to 410 mm and of "humpback" whitefish from 103 to 362 mm. Most collections covered a much narrower size range.

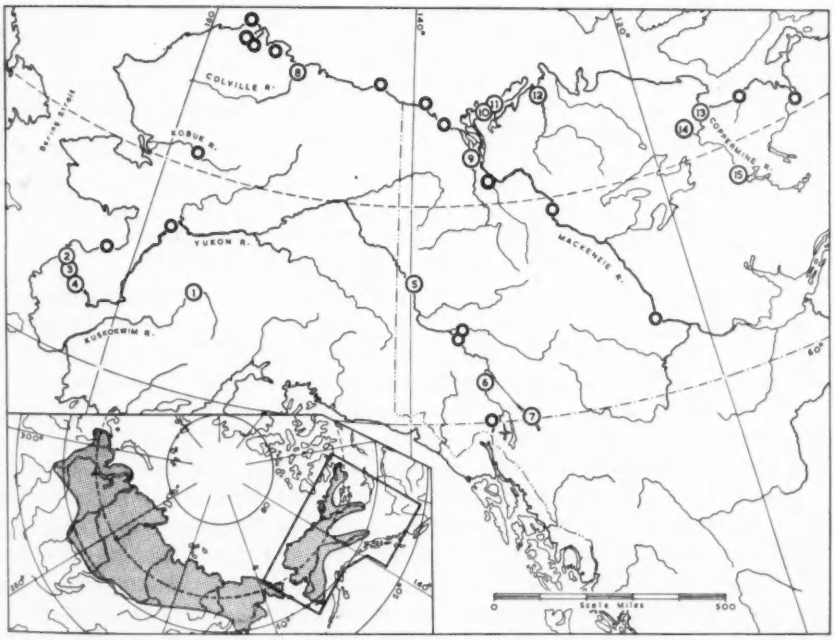

FIG. 1. Locality records of *Coregonus nasus*. Numbered circles (corresponding to Table I) show localities from which both *C. nasus* and "humpback" whitefish were examined in this study. Other circles are authentic literature records of *C. nasus*. Inset shows world distribution; Eurasian portion modified from Kulikova (1960). [N.B.: The southernmost unnumbered locality should be deleted — see the Addendum to this paper.]

Many other collections of "humpback" whitefish from within or close to the range of *C. nasus* were examined and found not to include the latter species. Counts and measurements on these fish have been considered in selecting the diagnostic features of *C. nasus*, but they are not included in figures presented here unless so stated. Such localities include:

ALSEK RIVER SYSTEM: Dezadeash Lake
COPPER RIVER SYSTEM: Paxson Lake
SUSITNA RIVER SYSTEM: Lake Louise
BRISTOL BAY DRAINAGES: Grosvenor Lake, Naknek Lake, Iowithla River, Wood River, Aleknagik Lake
KUSKOKWIM RIVER SYSTEM: Aniak
YUKON RIVER SYSTEM: Marshall, Nulato, Chatanika River, Cantwell, Tanana River, Lake Minchumina, Chisana River, Birch Lake, Circle, Old John Lake, Pickhandle Lake, Kluane Lake, Fox Lake, Takhini River, Lewes River, Atlin Lake, Swan Lake
NORTON SOUND: Unalakleet
SEWARD PENINSULA: Kuzitrin River
MACKENZIE RIVER SYSTEM: Summit Lake — Hart Highway, Wolverine Lake, Moberley Lake, Hay River, Great Slave Lake, Gordon Lake, Kakisa Lake, Lac la Martre, Beaverlodge Lake
COPPERMINE RIVER SYSTEM: Vaillant Lake
ELLICE RIVER SYSTEM: Ellice Lake
BACK RIVER SYSTEM: Macdougall Lake, Beechey Lake
CHESTERFIELD INLET DRAINAGES: Beverley Lake, Whitefish Lake, Dubawnt Lake, Wholdaia Lake, Angikuni Lake
MAGUSE RIVER SYSTEM: Maguse Lake
THA-ANNE RIVER SYSTEM: Hyde Lake.

TECHNIQUES OF COUNTS AND MEASUREMENTS

Data, unless otherwise stated, were obtained in the laboratory from specimens preserved in formalin and later transferred to alcohol. Counts and measurements were taken on the left side of the specimen where appropriate. Caliper measurements were made with dial calipers reading to 0.1 mm.

Gill raker count was obtained from the anterior left gill arch, dissected out and examined under magnification. Every bony rudiment was included. Failure to remove the arch or to use magnification has been found to result frequently in lower counts, particularly under inclement field conditions.

Dorsal fin ray count included only principal rays and excluded the anterior 2 to 4 short rays which are less than three-quarters the length of the longest ray. The last two rays arising from a common base were counted as one.

Lateral line scale count started at the first pored scale touching the pectoral girdle, and extended to the posterior end of the scaled portion of the body including those small scales behind the point marking the end of the "standard length". This count usually exceeds by about 3 scales the conventional lateral line scale count, which stops at the structural base of the caudal fin (Hubbs and Lagler, 1958).

Suprapelvic scale count, illustrated in Fig. 2b, started at the anteriormost scale showing (in part or in whole) above the dorsal free edge of the pelvic axillary scale, and proceeded upward and backward to but not including the lateral line.

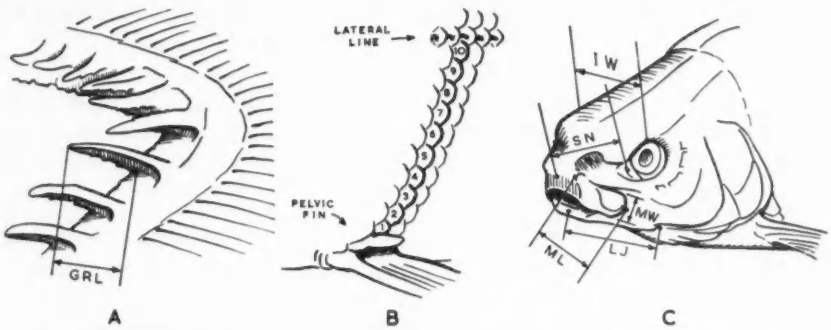

FIG. 2. Methods of measuring and counting. A—Lateral view of angle of anterior left gill arch showing method of measuring longest gill raker (GRL). B—Suprapelvic scale count on left side of fish (10 in illustration). C—Head measurements: interorbital width (IW), snout length (SN), maxilla length (ML), maxilla width (MW), length of lower jaw (LJ).

Caudal peduncle scale count was the number of horizontal scale rows intersecting an imaginary line around the narrowest part of the caudal peduncle.

Standard length was taken on a measuring board, from the tip of the snout to the structural base of the caudal rays (indicated by a crease when the tail was flexed), measured in a straight line and not over the curve of the body.

Maxillary length (Fig. 2c) was measured by seizing the maxilla with the jaws of the calipers. One jaw was placed snugly against the slight projection indicating the anterior of the maxillary bone. This measurement differs from "length of upper jaw", which is commonly measured from the tip of the snout and includes the premaxilla.

Maxillary width (Fig. 2c) was measured with the caliper jaws parallel to the length of the bone, grasping the upper jaw *in situ*.

Head length was measured by calipers from the tip of the snout to the posterior margin of the fleshy membrane of the opercle.

Interorbital width (Fig. 2c) was the least distance across the head between the orbits, with the caliper jaws tightened so as to displace the fleshy orbital margin but not distort the bones.

Gill raker length (Fig. 2a) was measured, using pointed calipers, from the tip to the base of the longest raker, with one caliper point inserted in the angle at the ventral side of the raker base.

Length of lower jaw was measured from the anterior tip of the lower jaw to the posterior angle of the mandible, with the blunt caliper jaw pushed into the soft flesh behind this angle (Fig. 2c) and the mandible squeezed firmly between the caliper jaws.

Head depth was measured with calipers from the occiput to the breast, perpendicular to the length of the body.

Peduncle depth was the least depth through the peduncle perpendicular to the length of the body.

Adipose fin length was measured from the angle between the anterior margin of the adipose fin and the contour of the body (*not* from the edge of scalation) horizontally back to the posterior free edge of the fin.

Pectoral fin length was measured by inserting one pointed caliper jaw ahead of the base of the longest pectoral ray and pushing it firmly backwards against the fin base, and placing the other jaw at the tip of the straightened longest fin ray.

DELINEATION OF THE PROBLEM

The broad whitefish, *Coregonus nasus*, is easily distinguishable from all other North American whitefishes excepting those in a restricted group of species within the genus *Coregonus*. In order to delimit which species are considered here to be involved in possible confusion with *C. nasus*, there follows an outline of the distinctive characters of other groups of whitefish.

The whitefishes comprise the family Coregoninæ according to some recent authors or the subfamily Coregoninæ or Coregonini within the family Salmonidæ according to others. Norden (1961) gives their osteological characters.

The following whitefish genera are recognized by Norden (1961). The inconnu genus *Stenodus* stands distinct from other North American Coregonids on the basis of several osteological features. The genus *Prosopium* has been alternately lumped with *Coregonus* or split off as distinct. The single nostril flap, presence of parr marks in the young, and certain other features have long been known to distinguish candidates for the genus *Prosopium*, but the differences have been judged by many authors to be insufficient to justify separating these species from the genus *Coregonus*. However, Norden (1961) has now demonstrated that all species of *Prosopium* also possess a basibranchial plate in the floor of the mouth (a bone absent in all species of *Coregonus*), as well as certain other osteological characters. Accordingly, the conservative view that the whitefish species *cylindraceum*, *coulteri* and *williamsoni* belong to a distinct genus *Prosopium* appears to be fully justified. Also included are *Prosopium spilonotus* (Snyder), *P. abyssicola* (Snyder) and *P. gemmiferum* (Snyder), species endemic to the Bonneville basin in the western United States.

The third genus of whitefishes, *Coregonus*, contains species with no parr marks, double nostril flaps, no basibranchial plate, and with other distinctive osteological characters. It includes those species which have until recently been split by many authors into the two genera *Coregonus* and *Leucichthys*. The latter group consists of the "ciscoes" or "freshwater herrings", which are pelagic plankton-feeders with large mouths, antrorse premaxillae and many gill rakers. These characters intergrade in degree between different species and within single species in different habitats and different sizes. Their possession, of obvious adaptative significance, may often indicate convergent evolution produced by similar selective pressures, rather than close phylogenetic relationship. Indeed, the Bonneville cisco, now called *Prosopium gemmiferum*, a plankton-feeding form with long gill rakers, was originally described as a *Leucichthys*, before the discovery of a basibranchial plate and characteristic supraethmoid bone showed

that the species had evolved from *Prosopium* rather than *Coregonus* stock (Norden, 1961).

Since the genus *Coregonus* is here considered to include *Leucichthys*, a large number of species are involved. The present purpose is to demonstrate that in North America the broad whitefish *Coregonus nasus*, is distinct from all other species of *Coregonus*. One group of species can be set aside immediately as not likely to be confused with *C. nasus*; these are the cisco-like or "*leucichthys*-like" fishes. In them the tip of the lower jaw is usually even with or projecting beyond the tip of the snout, with the premaxillae usually vertical or antrorse (i.e. the profile of the upper lip slopes downward and forward). The maxilla is long and usually ends beneath the pupil of the eye. The profile of the mouth and snout is not invariable—Walters (1955) describes specimens of *C. autumnalis* with retrorse premaxillae — but a gill raker count in excess of 32 may be taken as placing a species in the cisco-group for purposes of this discussion. Some Eurasian species, and some from the Great Lakes region, may have fewer than 33 gill rakers and yet possess terminal mouth openings and long maxillae. Hence, the cisco-group can be defined as species possessing *either* antrorse premaxillae, *or* 33 or more gill rakers, or both. Included will be the nominal species *C. artedii*, *C. autumnalis*, *C. sardinella*, a number of species from the Great Lakes area, and the Eurasian species *C. albula* and *C. oxyrhynchus* which have been suggested as possible synonyms of North American species (Svärdson, 1957). The cisco-group includes both the "*albula*-group" and the "*leucichthys*-group" of Gasowska (1960), who states that these species have distinctively shaped maxillae and premaxillae setting them off from other species of *Coregonus*.

Remaining are species of *Coregonus* with fewer than 33 gill rakers and invariably having retrorse premaxillae (i.e. the snout overhangs the tip of the lower jaw). These include on the one hand *C. nasus*, and on the other a group of species whose relationships are unclear. In this paper the latter group will be collectively known as "humpback" whitefish, because all the North American forms have a more or less well-developed nuchal hump producing a concave profile behind the head, in contrast to the distinctive convex rounded or "sheep-nosed" profile of *C. nasus*.

"Humpback" whitefish include in North America species which have been described by various authors as *C. clupeaformis*, *C. pidschian*, *C. lavaretus*, *C. nelsoni* and others. Some of these designations imply correspondence between New and Old World species which are unproven, and some may be synonyms. No attempt will be made in this paper to adjudicate on relationships between the various "humpback" whitefishes. Data on them are presented here only in order to demonstrate wherein they differ from *C. nasus*.

Coregonus nasus (Pallas), the broad, round-nosed or sheep-nosed whitefish, has commonly gone under the name *C. kennicotti* in the New World. It is said by Gasowska (1960) to have a distinctive maxilla and premaxilla of the "*paralavaretus*-type", but it has evidently been confused with other Eurasian species by Svärdson due to his reliance solely on gill raker counts. A discussion of synonymy is given at the end of this paper.

EVIDENCE FROM GENERAL APPEARANCE

Separation of specimens used in this study into two categories, broad whitefish (*C. nasus*) and "humpback" whitefish, has been based initially on their general appearance. Counts and measurements given in later sections refer to fish which have first been assigned to one or other category by subjective, qualitative appraisal. Later quantitative study has in every case confirmed the categorization. The only doubtful specimens seen have been a few very large whitefish, from beyond the geographic range of *C. nasus*, which superficially resembled the latter in having blunt heavy heads. Closer examination soon showed these to be "humpback" whitefish.

The shape of the head and snout are distinctive; the specific name *nasus* probably has reference to the characteristic "nose". The sheep-nosed look of *C. nasus* is apparent in the juvenile, adult and very large individuals in Fig. 3, and in the three pairs of adult heads from three other localities shown in Fig. 4. The sheep-nosed appearance is due to a foreshortening, deepening and widening of the front of the head in *nasus* relative to the "humpbacks", with concomitant changes in the size and proportions of the snout and maxilla. The profile is also distinctive. "Humpbacks" are concave at the nape of the neck, sometimes markedly so; *nasus*, although sometimes developing a slight concavity at the nape in large fish (Fig. 3), presents a generally convex profile from the dorsal fin to the tip of the snout.

The body of *nasus* is deeper throughout more of its length, and looks more "slab-sided" and less stream-lined, than that of the "humpback" (Fig. 3). The adipose fin is larger in *nasus*, sometimes strikingly so, and the peduncle is deeper. It has been claimed that in the Mackenzie delta *nasus* can be distinguished from "humpbacks" when the two are being removed from gillnets, as the tail of the former offers less of a "handle" to the grasp of the fisherman. The presence of two distinct forms is known to fishermen in many parts of the north, and has been commented on by scientists and explorers.

Other external differences, some of which are quantified in later sections, contribute to the totality of characters which allow recognition of *C. nasus*. Most characters, however, vary between localities and between fish of different sizes. This is true for "humpback" whitefishes as well as for *C. nasus*. The result is a surprising difficulty in locating a "key character" which makes possible positive identification of all specimens from all localities. Nevertheless, examination of collections from many places in northern Canada and Alaska leads to two conclusions: (i) that there are often two distinctive types of "non-cisco, non-*Prosopium*" whitefish living in the same place; (ii) that each pair includes a fish with characteristic "sheep-nosed" appearance, which is probably equivalent throughout the area and is referred to here as *C. nasus*. The quantitative assessment of these two statements occupies the next two sections.

COUNTED CHARACTERS

Three phenomena, exemplified by those characters which are summarized in Tables II and III, were found in all the counted characters studied.

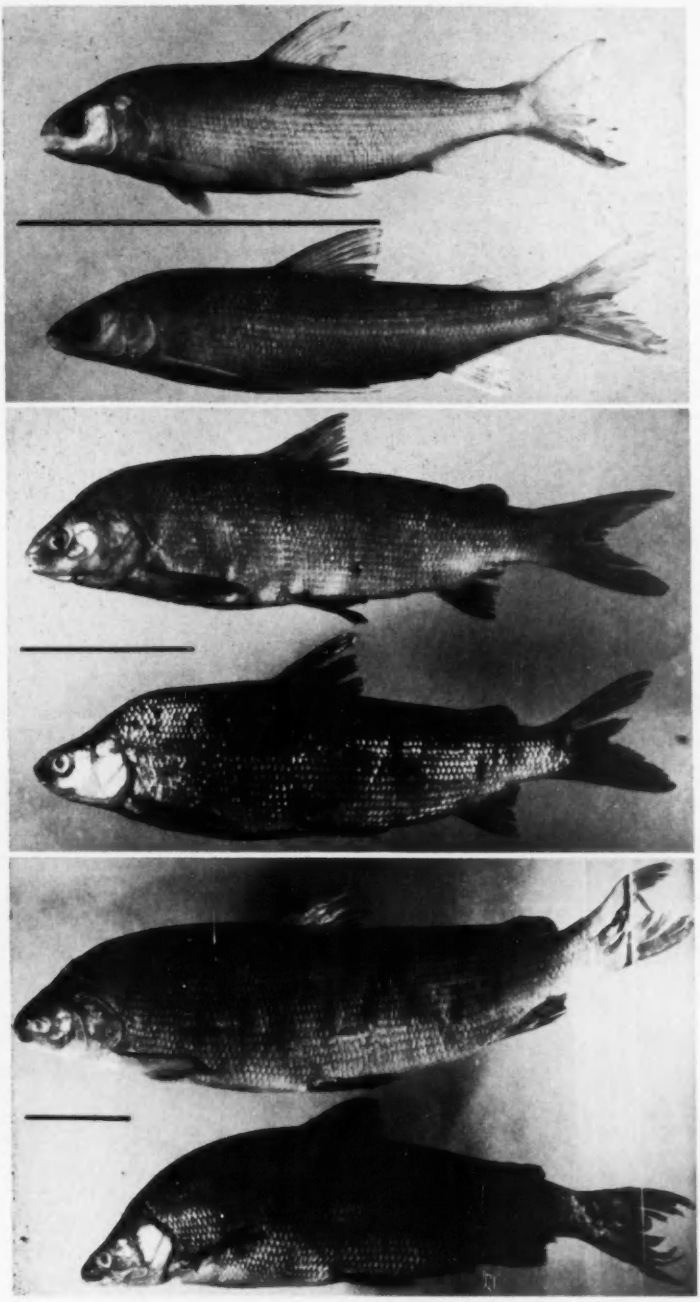

FIG. 3. Top specimen of each pair is *C. nasus*; bottom is a "humpback" whitefish from the same locality. *Top pair* (standard lengths 130 and 139 mm respectively) from Yukon River delta at Alakanuk. *Centre pair* (SL 304 and 301 mm) from lower Yukon River system at Andreafsky. *Bottom pair* (SL 550 and 502 mm) from Coppermine River system at Redrock Lake. Black line in each photograph is approximately 10 cm.

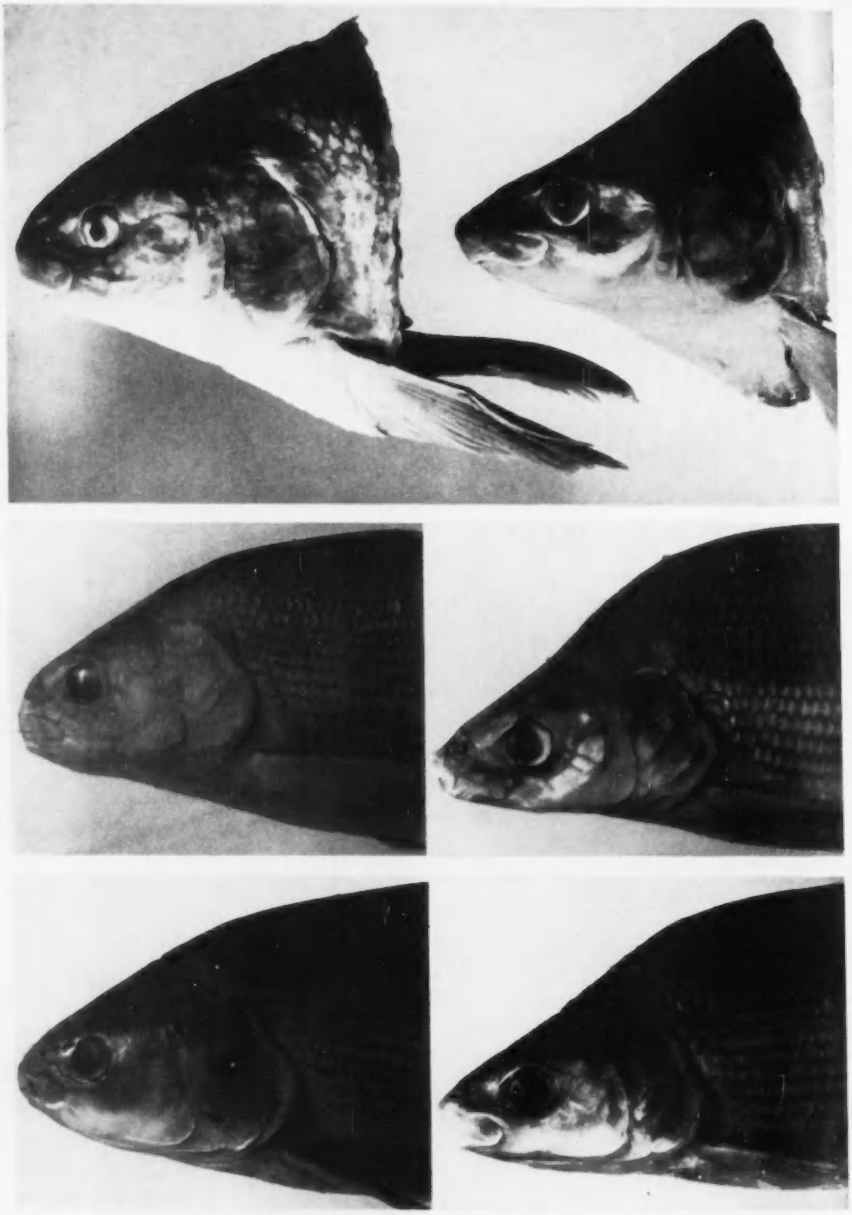

FIG. 4. Left hand specimen of each pair is *C. nasus*; right is a "humpback" whitefish from the same locality. *Top pair* (SL 530 and 490 mm) from Coppermine River system at Dismal Lake. *Centre pair* (SL 372 and 395 mm) from upper Yukon River system at Lake Laberge. *Bottom pair* (SL 311 and 324 mm) from Kuskokwim River at McGrath.

(a) Each character showed, in most or all localities, a significant difference between *C. nasus* and the local "humpback" whitefish.

(b) The direction of this difference, between *C. nasus* and the "humpback" species, was consistent for each character in most or all localities.

(c) Despite these significant and consistent differences, in every character there was sufficient overlap between the two species in at least some localities to preclude identification of all fish on the basis of that character alone.

TABLE II. Meristic counts of sympatric pairs of whitefish species.
C: *Coregonus nasus;* H: "humpback" whitefish.

Locality	Kind	Dorsal fin rays				Gill rakers											Suprapelvci scales			
		10	11	12	13	18	19	20	21	22	23	24	25	26	27	28	29	8	9	10	11
Kuskokwim	C	1	3	..	..	..	..	..	1	1	2	..	..	..	..	..	..	..	..	4	..
	H	..	..	2	1	..	..	..	1	1	..	..	..	..	..	..	..	2	..	..	..
Alakanuk	C	..	1	2	1	..	..	..	..	2	1	1	..	..	..	..	..	..	..	3	1
	H	..	..	7	3	..	..	..	..	..	..	1	4	3	2	..	..	4	6	..	..
Andreafsky	C	1	10	3	..	..	..	..	1	7	3	2	1	..	..	..	..	..	6	6	2
	H	..	3	6	1	..	..	..	..	..	2	5	3	1	1	..	..	5	5	..	..
Dawson	C	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..	1
	H	..	..	..	..	..	..	..	..	..	..	..	1	..	..	..	..	1	1	..	..
Laberge	C	1	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..	..	1	..
	H	..	3	3	..	..	..	..	..	..	..	4	1	..	1	..	..	4	2	..	..
Teslin[a]	C	3	1	..	..	..	..	..	..	..	5	9	3	..	..	..	..	..	..	3	1
	H	..	3	5	1	..	..	..	..	..	1	5	11	5	..	1	..	4	5	..	..
Colville	C	..	3	..	..	..	..	..	1	1	1	..	..	..	..	..	..	..	3	..	..
	H	..	1	..	..	..	..	..	..	..	..	..	1	..	..	..	..	1	..	..	..
Aklavik	C	..	..	1	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..	1	..
	H	..	3	3	3	..	..	..	..	..	..	2	4	2	..	..	..	..	8	..	..
Kittigazuit	C	2	2	1	..	..	..	..	..	1	2	1	1	..	..	..	1	..	..	3	3
	H	..	3	2	..	..	..	..	..	..	..	1	2	1	..	..	..	1	4	..	..
Tuktoyaktuk[b]	C	1	6	5	..	..	1	8	1	2	..	..	..	..	..	..	..	..	..	..	..
	H	..	1	6	4	..	..	1	..	2	6	2	..	..	..	..	..	..	..	..	..
Anderson[b]	C	6	57	26	2	1	15	22	27	19	5	1	..	..	..	..	..	..	..	..	..
	H	..	5	14	4	..	..	..	..	3	5	7	6	2	..	..	..	..	..	..	..
Coppermine	C	..	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..
	H	..	..	..	..	..	..	..	..	..	..	..	..	1	1	..	..	..	..	..	..
Dismal	C	..	3	..	..	..	..	..	3	2	6	2	1	..	..	..	..	..	3	..	..
	H	1	5	2	..	..	..	..	..	..	..	..	1	4	7	1	2	5	4	..	..
Redrock	C	..	5	2	..	..	..	..	2	..	4	1	..	..	..	..	..	..	1	2	1
	H	..	6	2	..	..	..	..	..	..	..	..	1	2	3	2	..	3	1	..	..

[a]Includes gill raker counts supplied by Dr W. A. Clemens.
[b]Gill rakers counted in field by M E. Riske without magnification.

GILL RAKERS

In Table II gill raker counts shown for Tuktoyaktuk and Anderson River were made by a field party without use of magnification, and therefore may not be directly comparable to other counts shown. Similarly some counts given in the literature might have been higher had all rudimentary rakers been counted under magnification. Svärdson (1957) states that counting whitefish gill rakers in the field invariably gave figures too low.

Gill raker counts of the *C. nasus* examined in the laboratory ranged from 21 to 25, and of the "humpback" from 21 to 29. Literature records extend these

ranges to from 19 to 25, and from 16 to 30, respectively, for all arctic North America (Walters, 1955). "Humpbacks" have appreciably more gill rakers than *C. nasus* in most north slope drainages of Canada and Alaska, but in Kotzebue Sound and Bering Sea drainages the overlap between the two is too great to allow identification on this basis.

In addition to counts shown in Table II, two specimens of *C. nasus*, one from Herschel Island and one from King Point on Mackenzie Bay, each had 24 gill rakers. These, combined with counts in Walters (1955) and in Table II, indicate an erratic geographic variation in gill raker count. Modal values vary from a high of 24 in Teslin Lake in the upper Yukon River (most southerly record in North America) to 20 in several localities along the Arctic Ocean. No consistent association is apparent between number of gill rakers and climate or distance from the sea. There is some suggestion of higher counts amongst lake and sea dwellers (plankton feeders?) than amongst permanent river dwellers, but knowledge of the food habits, and of possible migrations between rivers and lakes or the sea, is lacking. Eschmeyer and Bailey (1955) noted that lacustrine populations of *Prosopium coulteri* tended to have higher gill raker counts than did fluviatile populations.

Dorsal Fin Rays

Major dorsal fin rays (Table II) varied from 10 to 13 in both *C. nasus* and "humpbacks". Ray count averaged lower in *C. nasus* than in "humpbacks" in all but one locality, but overlap was great in most localities. Modal counts in *C. nasus* were lowest in the most southerly collection (Teslin Lake) and highest in the most northerly (Colville River), but erratic variation occurred between these extremes.

Scale Counts

A tendency towards higher scale counts in *C. nasus* than in sympatric "humpbacks" is demonstrated by suprapelvic and lateral line scale counts (Tables II and III), and also in the number of scale rows around the caudal peduncle (not shown). Of these, the suprapelvic count is easiest to make and gives the best separation. *C. nasus* had from 8 to 11 suprapelvic scales, while "humpbacks" had 8 or 9. Complete separation of all individuals on this basis was possible in some of the samples examined, but geographic variation again produced much overlap between the species. Nevertheless this is the most satisfactory meristic count examined. It can be applied to clear photographs or accurate drawings. Any fish with 10 or 11 suprapelvic scales is likely to be a *C. nasus*, but specimens with fewer cannot be identified by this count.

Counts of "total scales in the lateral line" (Table III) are not directly comparable to some published counts (e.g., Walters, 1955) which extend only to the structural caudal base. Total lateral line scales ranged from 84 to 102 in *C. nasus* and from 77 to 92 in "humpbacks", in specimens examined. As in suprapelvic scales, *C. nasus* had the higher average count in all but one localities, but overlap was sometimes great.

TABLE III. Lateral line scale counts of sympatric pairs of whitefish species. C: *Coregonus nasus;* H: "humpback" whitefish.

Locality	Kind	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98
Kuskokwim	C	..	..	..	..	..	..	..	..	..	1	..	1	..	1	..	..	..	1	..	..	..	..
	H	1	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Alakanuk	C	..	..	..	..	..	..	..	..	..	..	..	1	..	..	3	..	..	..	..	..	..	..
	H	..	..	1	..	..	1	1	1	2	1	1	1	1	..	..	..	..	..	..	..	..	..
Andreafsky	C	..	..	..	..	..	..	..	1	..	2	3	2	1	1	2	1	..	..	..	..	..	..
	H	..	..	..	1	1	2	..	2	1	2	..	1	..	..	..	..	..	..	..	..	..	..
Dawson	C	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..
	H	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..
Laberge	C	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	..
	H	..	..	..	..	..	..	3	..	1	..	..	1	..	..	..	..	..	..	..	..	..	..
Teslin	C	..	..	..	..	..	..	..	..	..	..	1	..	..	2	1	..	..	..	..	..	..	..
	H	..	..	..	2	..	1	2	1	..	..	1	1	..	1	..	..	..	..	..	..	..	..
Colville	C	..	..	..	..	..	..	..	..	..	..	..	..	1	1	1	..	..	..	..	..	..	..
	H	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Aklavik	H[a]	..	..	..	2	..	..	..	..	1	..	2	2	..	..	..	..	..	..	..	..	..	..
Kittigazuit	C	..	..	..	..	..	..	..	1	..	..	..	..	..	2	3	..	..	..	..	..	..	..
	H	..	..	..	..	..	..	..	1	2	..	1	..	..	..	..	..	1	..	..	..	..	..
Tuktoyaktuk[b]	C	..	..	..	..	..	..	1	..	1	1	1	1	2	1	1	3	..	..	..	..	..	..
	H	1	..	..	1	..	..	1	1	1	1	1	1	1	..	1	..	..	..	1	..	..	..
Anderson[b]	C	..	..	..	..	..	..	1	6	10	7	16	12	17	10	5	4	..	1	1	..	..	1
	H	..	..	1	..	1	1	1	2	5	7	2	..	1	1	1	..	..	..	..	..	..	..
Dismal	C	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	..	1	1	..	..	..	..
	H	..	1	1	..	1	..	4	1	1	1	..	..	..	..	..	..	..	..	..	..	..	..
Redrock	C[c]	..	..	..	..	..	..	..	..	1	1	..	..	..	1	1	2	..	..	..	..	..	..
	H	..	1	1	2	1	1	..	..	..	2	..	..	..	..	..	..	..	..	..	..	..	..

[a]Also one fish with 74 scales.
[b]Field counts by M E. Riske, increased by 3 to adjust for difference in counting method.
[c]Also one fish with 102 scales.

Scale rows around the caudal peduncle, not shown, displayed the same trend. Counts ranged from 25 to 29 in *C. nasus* and from 22 to 29 in sympatric "humpbacks." *C. nasus* averaged higher in every locality, but overlap made the count less satisfactory than suprapelvic scales in distinguishing species.

BRANCHIOSTEGAL RAYS

Branchiostegal rays were not counted on most specimens, but Dr W. A. Clemens has kindly provided counts from Teslin Lake fish. Of *C. nasus*, 9 had 8 rays and 3 had 9 rays; while of "humpbacks" only 3 had 8 rays and 9 had 9 rays. The tendency towards fewer branchiostegal rays in *C. nasus* is probably widespread, but there is clearly too much overlap in counts for this to serve as a method of identification.

MEASURED CHARACTERS

Body proportions, mostly associated with the maxilla or the gill rakers, have commonly been used as "key characters" to distinguish *C. nasus*. Relative rather than absolute size of body parts must be used if fish of different lengths are to be identified. Unfortunately the two measurements chosen to be related (often standard length of the specimen and length of a body part) usually do not grow isometrically, and a proportional value which will separate species at one size may not be effective at another.

In this study many key characters given in the literature have been found ineffective for either very small or very large specimens. Accordingly, in searching for improved methods of identification, the growth of each part was first plotted relative to standard body length. Pairs of characters were then selected in which non-isometric growth of one was compensated for by non-isometric growth in the other in such a way that the two expressed as a proportion could distinguish between species at any size. Proof of the effectiveness of any of these pairs of characters is of course limited to the particular specimens available; although a wide total size range was examined, only part of the size range was covered by specimens from any one locality.

Maxilla Length and Standard Length

Length of the maxilla is only slightly greater in small "humpbacks" than in small *C. nasus*, but as standard length increases the divergence increases (Figs. 3, 4). "Humpbacks" show roughly isometric growth of the maxilla, while in *C. nasus* the maxilla becomes relatively smaller in large fish (Fig. 5). Even amongst large fish there is some overlap between the species; in the small individuals available the maxilla length as a percentage of standard length was wholly ineffective as a means of species separation. Values ranged from 3.9 to 5.5% in *C. nasus* and from 4.6 to 6.0% in "humpbacks".

Maxilla Length Relative to Eye

Jordan and Evermann (1896) describe the maxillary of the broad whitefish as "reaching slightly beyond the vertical from front of eye"; in contrast, Walters' key (1955) reads "maxillary ends at or before vertical of anterior edge of eye" for this species. Figs. 3 and 4 show that both conditions exist, in specimens from different areas, and the character is therefore invalid for distinguishing *C. nasus*.

Snout length, obviously associated with the character described above, is also ineffective for specific separation. Snout length varied from 3.8 to 5.6% of standard length in *C. nasus* examined, and from 4.0 to 5.9% in sympatric "humpbacks". "Humpback" snouts averaged longer in all localities, but much overlap occurred between the species.

Maxilla Length and Head Length

Head length plotted against standard length (not figured) displayed a different pattern from maxilla length. Specimens of *C. nasus* have longer heads than have "humpbacks" at small and intermediate sizes. Decelerated growth of head relative to standard length among large *C. nasus* produces convergence between the species. Because the specific differences in maxilla length and in head length are in opposite directions, and because the differences produced by relative growth tend to cancel one another, it might be hoped that maxilla length expressed as a proportion of head length would be a useful character. Berg (1948) uses "maxillary length less than 22% of head length" as a key character to separate *C. nasus*.

Although maxilla length expressed as a percentage of head length was found to produce better separation than either measurement expressed in terms of

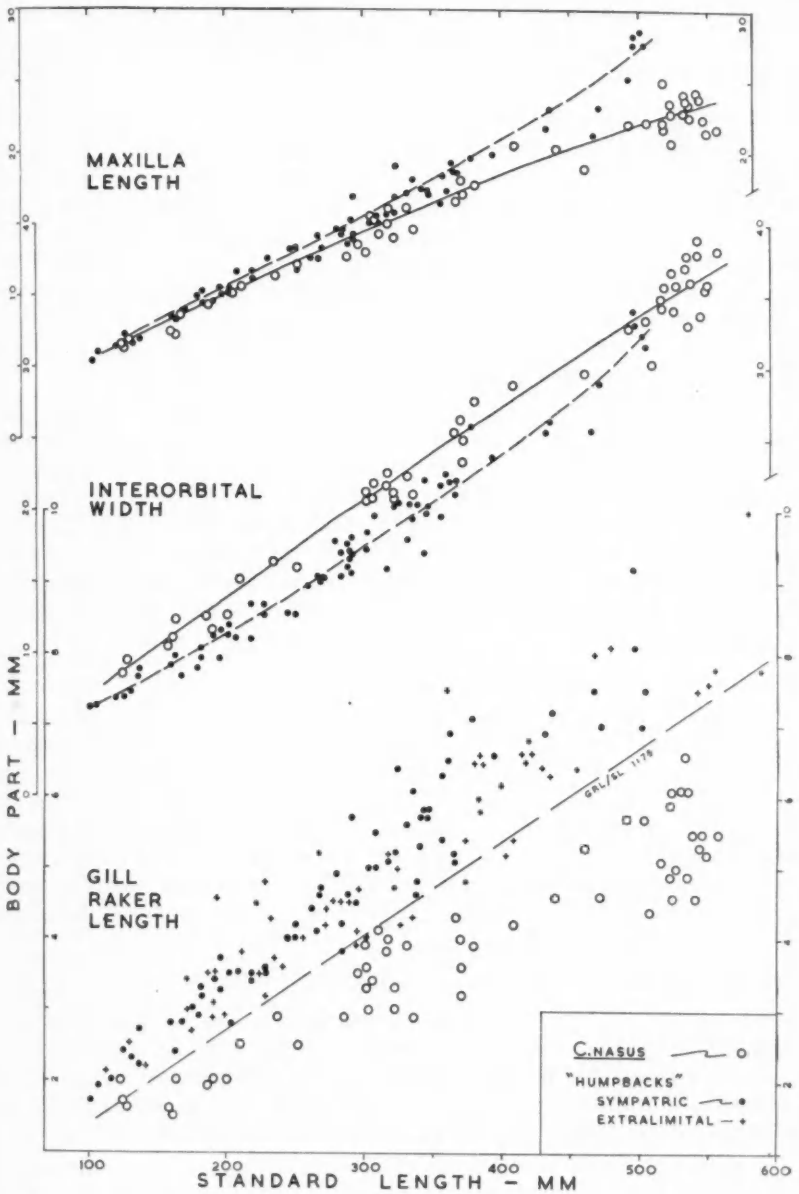

FIG. 5. Growth of three body parts plotted against standard length. Lines for maxilla length and interorbital width fitted by eye.

standard length, there was still too great an overlap to recommend it as a "key character". Specimens of *C. nasus* had values varying from 19.3 to 22.9% and "humpbacks" from 22.3 to 27.9%. Overlap did not occur in Coppermine River samples but was considerable in samples from the lower Yukon River.

Maxilla Length and Maxilla Width

Several authors have been aware that the maxilla is wider relative to its length in *C. nasus* than in "humpback" species, but the critical proportions given for identification have been inconsistent. Berg (1948), Walters (1955), and Wilimovsky (1958) describe *C. nasus* as having a maxillary length less than twice its width, and "humpback" species as having more than twice. Gasowska (1960) however, gives these proportions as 2.4 and 3.4–4.5 respectively. Inconsistencies may be due to differing procedures in measuring, such as measurement to the tip of the snout rather than to the anterior of the maxillary bone, or use of a maxillary bone separated rather than *in situ*.

Maxilla lengths plotted against maxilla widths (not figured) demonstrated that while there was large average difference in proportions between the species, there was also slight overlap. According to the techniques of measurement used here the best proportion to separate the species was 2.4. However, *C. nasus* ranged from 1.9 to 2.6 and "humpbacks" from 2.2 to 2.9. Overlap was not confined to specimens of a particular size range. Of characters so far described this is the most useful in distinguishing *C. nasus*, provided all measurements are made by one person, but it is still not completely effective, and is evidently subject to much personal bias.

Interorbital Width and Standard Length

Interorbital width plotted against standard length (Fig. 5) resembles head length in that the two species differ at small and intermediate lengths but converge at large sizes. Here *C. nasus* shows almost isometric growth over the sizes studied, while "humpbacks" display a gradually accelerating growth of interorbital width relative to standard length. At small and intermediate lengths separation is better in this character than in head length, but complete overlap amongst large fish precludes the use as a key character of interorbital as a percentage of standard length. Values ranged from 5.9 to 7.6% for *C. nasus* and from 4.9 to 6.9% for "humpbacks".

Maxilla Length and Interorbital Width

The species considered differ in opposite directions with regard to maxilla length and interorbital width, and convergence at large size in one character is balanced by divergence in the other (Fig. 5). Consequently, maxilla length expressed as a proportion of interorbital width gives a better separation of the species than does either expressed relative to standard length (Fig. 6).

Differential growth prevents the use of a single proportion to achieve complete separation of fish of all sizes. However, almost all specimens over 25 cm standard length (about 11 inches fork length) can be identified as either "humpback" whitefish or *C. nasus* depending on whether the maxillary length

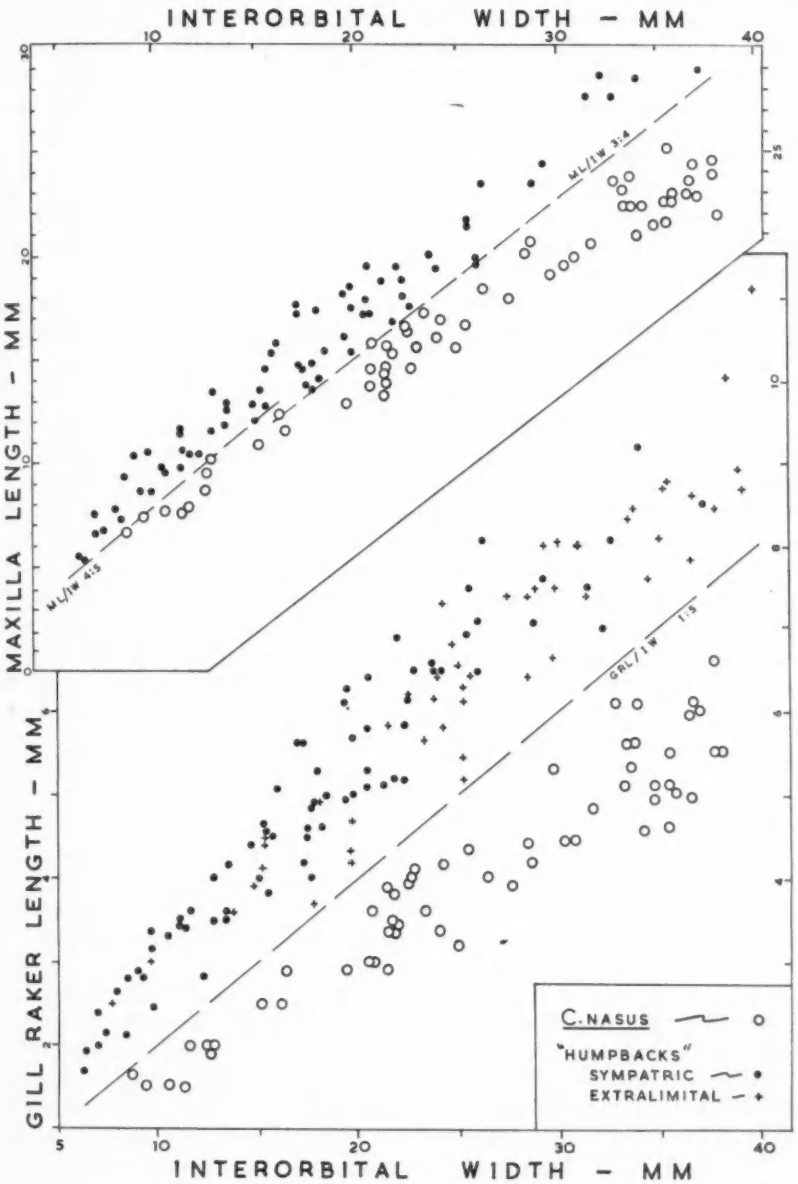

FIG. 6. Growth of two body parts plotted against interorbital width. Broken lines indicate best proportions for distinction of *C. nasus*. (Some points are based on heads, not whole specimens, and have no equivalents in Fig. 5.)

is more or less than $\frac{3}{4}$ of the interorbital width. Fish under 25 cm standard length can also be separated if $\frac{5}{8}$ rather than $\frac{3}{4}$ be taken as the dividing line. Lines on Fig. 6 correspond to these proportions. *C. nasus* less than 25 cm SL had maxillary length to interorbital width ratios from 0.76 to 0.80, while humpbacks of this size ranged from 0.81 to 1.05. Above 25 cm SL, *C. nasus* ranged from 0.66 to 0.75, and humpbacks from 0.75 to 1.00.

The use of different critical proportions for different sized fishes is inconvenient. Nevertheless, it is possible on this basis to correctly classify all but 3 of the specimens available as either *C. nasus* or "humpbacks". Maxilla length length as a proportion of interorbital width is therefore the most effective of characters so far discussed. It is also based on measurements conveniently made in the field on whole specimens. Characters discussed later which depend on gill-raker length produce wider separation between the species, but are not so convenient to measure under adverse conditions.

Gill Raker Length and Standard Length

Walters (1955) states that the gill raker length can be divided about 75 to 100 times into the standard length in *C. nasus*, but less than 70 times in what are here called "humpbacks." According to my measurements (Fig. 5) many "humpbacks" have gill rakers dividing more than 70 times into the standard length. This is particularly true if "humpbacks" from Bristol Bay or upper Yukon River areas just outside the known range of *C. nasus* are included (marked by crosses on Fig. 5). Methods of measuring gill raker length vary, but even when all measurements are made in the same way there is slight overlap between *C. nasus* and sympatric "humpbacks" of small and intermediate size. Decelerated growth of gill raker length in large *C. nasus* produces complete separation between these and large "humpbacks." Gill raker length as a percentage of standard length ranged from 0.85 to 1.35% for *C. nasus* and from 1.32 to 1.97% for sympatric "humpbacks". The line giving best (but not complete) separation of the two types shown in Fig. 5 represents 1.33%, or "gill raker length 75 times into standard length".

This is an unsatisfactory "key" character, because of the lack of separation at all sizes, the subjectivity of measuring gill raker length, and the necessity of knowing standard length (requiring whole specimens, not always obtainable for large fish from remote areas). An example from the literature will illustrate. Dymond (1943) published gill raker lengths of 11 whitefish specimens from Kittigazuit, along with standard lengths which had to be estimated largely from skins rather than whole specimens. Walters (1955) concluded from these measurements that the collection contained 4 *C. nasus* and 7 *C. clupeaformis*. I have re-examined the specimens, from the Royal Ontario Museum, and find they consist of 6 *C. nasus* and 5 "humpbacks" (*C. clupeaformis*?) identifiable by several different criteria (given in this paper) which are independent of knowing the standard length. The previous misplacement of two of the specimens arose from a compound of the three sources of error named.

Despite these arguments against its use as a means of identification, there is certainly a large average difference in gill raker length between the species at all

sizes (Fig. 5). Svärdson (1957) objected to use of gill raker length because it is correlated with gill raker number. While in most areas studied *C. nasus* has fewer gill rakers than "humpbacks" (Table II), raker length still differs widely between the two species occurring sympatrically in a few places (Kuskokwim, Aklavik) where *C. nasus* in the samples do *not* have fewer gill rakers. At least in these areas there is a specific difference in raker length not attributable to difference in raker number.

Gill Raker Length and Interobital Width

Growth characteristics of interorbital width have already been described. Convergence between the species in this character can be counterbalanced by the divergence shown in gill raker length (Fig. 5). Gill raker length plotted against interorbital width (Fig. 6) was found to give complete separation between all *C. nasus* and all "humpbacks". Figure 6 includes measurements (shown as crosses) of some "humpback" specimens from localities, listed under Material, which are beyond the geographic range of *C. nasus*. Even relatively short-rakered specimens of "humpbacks" are separable from all *C. nasus*. The line in Fig. 6 marks a ratio of 1 to 5; all *C. nasus* have gill rakers less than 20% of the interorbital width (range 13 to 19%); all sympatric "humpbacks" have gill rakers longer than this (range 22 to 34%).

This was the most effective single proportion found for laboratory identification of the species. Measurement of gill raker length under field conditions is inconvenient in contrast to measurement of maxillary length, but a greater margin of error is tolerable because of the wide separation in this ratio between *C. nasus* and related whitefishes.

Gill raker length has been expressed by other methods. Wynne-Edwards (1952) describes the gill rakers of the broad whitefish as "less than half the height of the adipose fin", and Walters (1955) says of this species that the longest gill rakers are less than the diameter of the pupil of the eye. The great changes in relative size of both adipose fin and eye with body size are visible in Fig. 3. Accurate measurement of either is sometimes difficult. Interorbital width is a more precise and satisfactory character to combine with gill raker length in distinguishing *C. nasus*.

Length of Lower Jaw and Standard Length

The lower jaw of the "humpbacks" studied showed almost isometric growth, while the jaw of *C. nasus* displayed marked negative allometry. In small fish the jaw is slightly longer in *C. nasus* than in "humpbacks", but in very large fish growth rate of the jaw in *C. nasus* has so decreased that the species has now a very much shorter jaw than have comparable "humpback" whitefish. Lower jaw length is therefore not useful in distinguishing the species concerned, and should be used only with caution in such keys to other whitefishes as that of Gasowska (1960). Lower jaw length as a percentage of standard length ranged from 6.4 to 8.4% in *C. nasus* and 6.9 to 8.6% in "humpbacks".

Head Depth and Associated Characters

The head in *C. nasus* is not only longer but also deeper than in "humpback" whitefish (Figs. 3, 4). Head depths expressed as percentage of standard lengths ranged from 14 to 18% in *C. nasus* and from 12 to 16% in sympatric "humpbacks". Overlap between the species was considerable in some localities, and the character is therefore not useful in identification.

The distance between the eye and maxilla is notably greater in *C. nasus* than in "humpbacks" of certain sizes and from certain localities (Fig. 4, and Wynne-Edwards, 1952). Shorter maxilla and deeper head, in *C. nasus*, contribute to this effect. However, the width of the actual suborbital bone differs less markedly between the species. The character is ineffective in identifying all individuals from all localities.

The deeper head of *C. nasus* is associated with differences in shapes of the opercular bones. Wynne-Edwards (1952) pointed out that the preopercular margin is more sharply angled than in "humpbacks"; the differences are visible between each pair of heads in Fig. 4. The character is difficult to quantify, and is not diagnostic in small specimens (Fig. 3).

Peduncle Depth and Standard Length

The caudal peduncle of *C. nasus* is relatively deep (Fig. 3), sometimes very noticeably so, in contrast to "humpback" whitefish of the same size. Plots of peduncle depth against standard length (not given) showed divergence between the species to be greatest at intermediate sizes, with considerable overlap in the shortest and longest fish studied. Peduncle height as a percentage of standard length ranged from 8.0 to 10.5% in *C. nasus* and from 7.5 to 10.4% in sympatric "humpbacks". Overlap is too great to make the character taxonomically useful.

Adipose Length and Standard Length

The adipose fin is strikingly well developed in some specimens of *C. nasus*; in some localities it is much larger than in sympatric "humpbacks", while in others there is very great overlap between adipose size of the two species. Adipose fin length as a percentage of standard length ranged from 8.5 to 13.2% in *C. nasus*, and from 7.5 to 11.4% in sympatric "humpbacks". Overlap was least in Coppermine River drainages and most in the lower Yukon River.

Length of Fins and Standard Length

In most localities the pectoral fin length was greater in *C. nasus* than in "humpbacks", but there was often great overlap. Pectoral length as a percentage of standard length ranged from 17 to 21% in *C. nasus* and from 14 to 19% in sympatric "humpbacks".

Length of pelvic fin, and height of anal fin, were also greater in *C. nasus* than in "humpbacks", according to measurements from Teslin Lake specimens provided by Dr W. A. Clemens. However, in both characters in both species the fins were appreciably longer in males than in females. The additional variability due to sexual dimorphism decreases the probable usefulness of these characters in distinguishing between species.

SUMMARY OF COUNTED AND MEASURED CHARACTERS

All of the counted characters which were examined differed significantly between the two types of whitefish, in a direction consistent for each character in most localities. Overlap was too great, however, to allow identification of all individuals on the basis of any one of the counted characters studied. The most useful was suprapelvic scale count; all *C. nasus* had counts of 8 or more, while all sympatric "humpbacks" had 9 or fewer. In other counted characters, greater overlap precluded their usefulness as "key" characters.

Many measured characters differed significantly between the two types, in directions consistent in different localities. However, most showed non-isometric growth (when plotted relative to standard length) in one or both types of fish; hence, in each character studied, convergence amongst either small or large fish prevented identification of all individuals on the basis of any one measurement expressed as a proportion of standard length. All such methods previously offered as "key characters" failed in correctly identifying some of the specimens studied.

One combination of measurements was found which, because of compensatory changes in growth, allowed correct identification of every specimen studied, including "humpbacks" from northern Canada and Alaska beyond the geographic range of *C. nasus*. Length of the longest gill raker was less than one-fifth the interorbital width in all *C. nasus* at all sizes seen; it was more than one-fifth in all "humpback" whitefish.

A second combination is somewhat less effective but more convenient for field identification. Maxillary length is less than three-quarters the interorbital width in *C. nasus*, more in "humpbacks"; for specimens under 25 cm standard length (about 11 inches fork length) the critical proportion should be increased to four-fifths. This combination correctly separated 98% of the fish studied.

Both combinations described have an additional advantage over measurements expressed in terms of body length, in that they may be used on incomplete specimens (skins, heads etc.). Methods of measuring are not consistent with all workers; the proportions given above must be measured according to the methods described in this paper and illustrated in Fig. 2.

NOMENCLATURE AND DISTRIBUTION

Pallas named *Salmo* (*Coregonus*) *nasus* from the Bay of Ob in 1776. Reference, in his latin description, to the thick head and thick body, single out this from the related species he described from the same area as being the broad whitefish. Günther's catalogue (1866) includes the broad whitefish as *Coregonus nasus* (Pallas). A list of references to *C. nasus* in Europe and Russia is given by Berg (1948). To these should be added Kulikova (1960) who gives many counts and measurements on *C. nasus* in the Yamal region north of the Ural Mountains, and Gasowska (1960) who discusses the shape of the maxilla in several whitefish species.

In North America Dall (1871) lists from Alaska the "Broad white-fish, *Coregonus muksun*, (Pallas,) Gunth." said to have a broad body and short head. That Dall referred to the broad whitefish now called *C. nasus* is shown by a figure of his specimen from Nulato, published by Turner in 1886; its identity is unmistakable. Dall, however, used the wrong scientific name; the muksun whitefish *Coregonus muksun* (Pallas) of north central Russia has from 44 to 72 gill rakers (Berg, 1948) and is apparently absent from the New World. Dall (1871) also refers to the "Round-fish. *Coregonus nasus*, (Pallas,) Gunth." as long, slender and subcylindrical. Bean (1887) corrects this and other scientific misnomers in Dall's paper, identifying Dall's "round-fish" as what is referred to now as the round whitefish *Prosopium cylindraceum* (Pallas).

The first detailed description of the broad whitefish in North America is credited to J. W. Milner in Jordan and Gilbert (1883), and is based on specimens from Fort Good Hope on the Mackenzie River and from the Yukon River in Alaska. Milner named it *Coregonus kennicotti*, described as "a strongly marked species, well distinguished among the American forms by the very obtuse head, but perhaps identical with some Siberian species". Slightly earlier, the name *Coregonus Kennicottii* Milner is listed by Bean (1881), without description, as occurring at Fort Good Hope and Nulato.

The name *C. kennicotti* (sometimes terminating in *ii*) is used by the following authors, who add the distribution records shown: Murdoch, 1884 (rivers near Point Barrow); Turner, 1886 (figure of specimen from Nulato, Yukon River); Townsend, 1887 (middle Kowak (Kobuk) River); Nelson, 1887 (St. Michael and Kuskokwim River); Bean, 1887 (Kotzebue Sound); Bean, 1890 (Meade River); Gilbert, 1895 (Mackenzie River delta); Scofield, 1899 (Barter Island); Fowler, 1904 (*C. kennicotti* from Meade River and Point Barrow, misidentified as *C. nelsonii*, corrected by Fowler, 1905); Evermann and Goldsborough, 1907 (Lake Bennett).

Clemens *et al.* (1945) report a "sheep-nose" as well as a "humpback" form of whitefish in Teslin Lake; the former is recognized in Teslin Lake as *C. nasus* by Walters (1955) and Carl *et al.* (1959).

Wynne-Edwards (1947) calls this species the "Mackenzie whitefish" and records it from Lake Laberge and Minto Lakes (p. 18); later (1952) he points out that the "Mackenzie broad whitefish" is the same species as the Siberian "chir" *C. nasus*, and names the North American form *C. nasus kennicotti*. He also records it from Pelly Crossing in Yukon Territory and in the Mackenzie River at Arctic Red River and as far upstream as Camsell Bend. Cohen (1954) describes age and growth of *C. nasus kennicotti* from Point Barrow.

Walters (1955) presents data indicating that Eurasian and North American specimens do not differ significantly and should therefore all be referred to as *C. nasus*. He adds records from Bathurst Inlet, Teshekpuk Lake, Alaktak River, Colville River; and earlier from Tree River (Walters, 1953).

Comparison of the present data with those of Walters (1955) and of Kulikova (1960) confirms that the broad whitefish of Eurasia and of North America do not differ significantly in any known character, and should be considered the same species.

The broad whitefish has been assigned by some to the genus *Prosopium*. Jordan and Gilbert (1883) listed *kennicotti* under the subgenus *Prosopium* of the genus *Coregonus*. Jordan, Evermann and Clark's 1930 checklist gave *Prosopium* generic rank and listed *Prosopium kennicotti* (Milner) from, among other places, "Lake Bennett, Alaska" (presumably Bennett Lake in British Columbia and Yukon Territory). Dymond (1943) gives the history of these generic changes.

Great Bear Lake Record

An erroneous record of the broad whitefish occurring in Great Bear Lake appears in the literature with mesmeric insistence. In 1895 Gilbert published "notes on fishes from the basin of the Mackenzie river in British America". His notes on *C. kennicotti* are based on a single skin from the delta of the Mackenzie River, presented by Miss Elizabeth Taylor. Included is the statement "The colour must have been very dark in life. Fins all blackish; in spirits with a bluish tinge." Jordan and Evermann (1896) quote this sentence but wrongly attribute it to a specimen "obtained by Miss Elizabeth Taylor in Great Bear Lake". The error may be due to the fact that on the same page with this sentence in Gilbert (1895) is a description of 2 specimens of *C. lucidus*, obtained by Miss Taylor, which were from Great Bear Lake. Evermann and Smith (1896) also quote the sentence concerning colour under *Coregonus kennicotti* and say "it was recently obtained by Miss Elizabeth Taylor in Great Bear Lake". Scofield (1899), referring to a specimen of *C. kennicotti* from Barter Island, says "We have compared it with a specimen obtained by Miss Elizabeth Taylor in Great Bear Lake and find they are the same. A description of the specimen obtained by Miss Taylor has been published by Dr. Gilbert, Bull. U.S. Fish Commission, 1894, 23." More recently Walters (1955) says "Gilbert (1895) listed the species for Great Bear Lake (as *C. kennicotti*)", which is not so.

An attempt to check Miss Taylor's specimen has been unsuccessful. Dr. Warren Freihofer reports that the Leland Stanford, Jr., University museum number 808, given by Gilbert (1895) for the whitefish in question, now corresponds to a Mexican cyprinodont. The original specimen may possibly have been destroyed by earthquake.

Recent surveys suggest that *C. nasus* does not in fact occur in Great Bear Lake. Kennedy (1953) says that during the survey of that lake by the Fisheries Research Board of Canada three species of coregonids were taken, and as far as could be determined no other species are present in the lake. These were the round whitefish, a cisco, and the lake whitefish or humpback "*C. clupeaformis*". During the survey 271 of "*C. clupeaformis*" were taken, from three widely separated parts, the only places where whitefish were found or reported in any quantity. Detailed taxonomic data (Kennedy, 1953) show no suggestion of the presence of *C. nasus*.

In short, the specimen of broad whitefish which gave rise to the records of this species from Great Bear Lake had probably never actually been there[2].

[2]Miss Taylor did not visit Great Bear Lake herself. For an insight into this woman's remarkable trip to the Mackenzie delta in 1892, the interested reader is referred to The Beaver (House organ of Hudson's Bay Co.): Outfit 278 (March 1948), pp. 19–23; Outfit 279 (June 1948), pp. 42–46.

Beauvert Lake Record

A puzzling single specimen of whitefish taken from Beauvert Lake in Jasper National Park, Alberta, was described by Bajkov (1927) as *C. nasus*. This isolated record is from the Mackenzie River basin but is some 1200 miles upstream of the nearest recorded occurrence of *C. nasus* (Camsell Bend); the two localities are separated by well-fished and well-studied waters (including Lake Athabasca and Great Slave Lake) where the species is apparently absent. Berg (1932), recognizing that Bajkov's fish had more gill rakers and fewer scales than the typical *C. nasus*, proposed a new subspecies *C. nasus canadensis*. Dymond (1943) obtained a second whitefish specimen from Beauvert Lake and published data which demonstrate that it was a "humpback" and not *C. nasus*, according to the criteria given in the present paper. (Diagnostic characters which place Dymond's specimen decisively as a "humpback" are gill raker count, and maxilla length as a proportion either of standard length or of interorbital width.)

Nevertheless, Bajkov's specimen was illustrated by two clear photographs, which can be used to check some of the measurements given. His gill raker counts (26, 27) and lateral line scale counts (81, 83, which include scales on the peduncle judging from the photograph) lie just outside the range of *C. nasus* given in Tables II and III of the present paper. Taken alone, these would identify the fish as a "humpback". On the other hand, maxilla length (as a proportion of standard length, of head length or of interorbital width), and peduncle depth as a proportion of standard length, all lie completely outside the ranges for "humpbacks" given in this paper, and would identify the fish as *C. nasus*. Maxilla length, head length, peduncle width, and (with reservations) standard length, were all confirmed by measurements on the photographs. (Bajkov's published measurement of snout length is in obvious error as checked against his illustration.)

The Beauvert Lake specimen was larger (about 57 cm SL) than any seen in the present study, and may owe its *nasus*-like characters to this fact. The illustrations show a profile roughly intermediate between the two large specimens from Redrock Lake illustrated in Fig. 3. The preopercular margin in *nasus*-like in its acuteness; the adipose fin is apparently small as in a "humpback". No information is given on gill raker length. Professor J. A. McLeod of the University of Manitoba has kindly tried to locate the specimen, but reports that apparently it has been lost.

That *C. clupeaformis* may be modified by the environment so as to superficially resemble *C. nasus* is demonstrated by 4 specimens in the Royal Ontario Museum (ROM 1224 to 1227). These fish were reared throughout life in the New York Aquarium, and have been described by Koelz (1929). Their markedly rounded head profiles and large adipose fins produce a striking similarity to *C. nasus*, yet their gill raker lengths expressed as proportions of their interorbital widths conform to their known parentage, *C. clupeaformis*.

In summary, Bajkov's single specimen lies outside the recorded range for *C. nasus* in scale and gill raker counts, and is highly disjunct geographically. Its resemblance to *C. nasus* in some body proportions may be due to its great

size, and perhaps to its environment (an elevation of 3356 feet, in a mountain climate). It might conceivably have originated from a hatchery. Without further data, I do not believe that the nominal subspecies *Coregonus nasus canadensis* Berg should be considered as valid.

Possible Synonymies

In early North American literature several synonymies are suggested between the broad whitefish and other species. *Coregonus richardsoni* Günther was variously suggested as a synonym of either *C. kennicotti* or perhaps *C. nelsonii* (Jordan and Evermann, 1896) or of *C. clupeaformis* (Jordan *et al.*, 1930). These problems did not, however, arise from doubting the existence of at least two sympatric whitefish species. Early authors customarily stressed the distinctness of the broad whitefish, even if they were not agreed as to its name.

In contrast, Dymond (1943) records that "in a number of areas in the northwest, a "crooked back" or "humpback" whitefish is distinguished from the more common form by the local people". However, Dymond examined specimens of both types, and concluded by synonymizing *C. clupeaformis* and *C. kennicotti*, saying: "Further research based on more adequate material may reveal differences between the so-called humpback and common whitefish[3] of the northwest that merit nomenclatural recognition, but such differences are not shown by the material now available." Wynne-Edwards (1952) and Walters (1955), on the contrary, stated that *C. nasus* could be distinguished by shorter gill rakers, shorter maxillary length etc. After re-examining specimens from the Royal Ontario Museum, I concur with Walters (1955) that Dymond's collections from Kittigazuit and from Peel River above Aklavik each contain two species.

More recently, Svärdson (1957) has reviewed the systematics of Eurasian species with the belief that only gill rakers (and occasionally spawning time) are reliable specific characters in whitefish. He suggests on this basis that *C. clupeaformis*, amongst others, is a synonym for *C. nasus*. Gasowska (1960), and the present author, challenge this view. Similarity of gill raker count does not mean that all populations placed by Svärdson under "*C. nasus*" are necessarily one species, and some of his suggested synonymies are unacceptable. Svärdson's "*C. nasus*" of Europe is probably not that species; the broad whitefish apparently has its western Eurasian limit in the Pechora River draining the west slope of the Ural Mountains (Kulikova, 1960).

Summary of Distribution

The broad whitefish of Eurasia and of North America is evidently the same species. Distribution records in the New World have been listed and examined critically in the foregoing sections. Accepted records are shown by circles in Fig. 1. These and the Eurasian distribution (in part from Kulikova, 1960)

[3]Some have construed this statement to mean that Dymond considered northwestern humpback whitefish as distinct from the species long known as *Coregonus clupeaformis* in central and eastern North America, in which region it was formerly often called the "common whitefish". However, Dymond's sentence can also be interpreted as meaning that he regarded the putative *nasus* type as "the common whitefish *of the northwest*".

have been combined in the insert in Fig. 1 to represent the world distribution of *Coregonus nasus*. Kulikova's map indicates an apparent gap in distribution of the species on the eastern tip of Siberia. This gap has been omitted in Fig. 1, as *C. nasus* has been reported from Achchen near the southern tip of the Chukotsk Peninsula (Barsukov, 1958) and the Bay of Korf on Bering Sea (Walters, 1955).

Briefly, the total range of *C. nasus* is: in Eurasia, in Arctic Ocean drainages from the Pechora River east across Siberia to Bering Strait, and south on Bering Sea to the Bay of Korf, and in the Penzhina River on the Sea of Okhotsk. Ascending the great Arctic Ocean drainages of Russia only to a short distance south of 60°N.

In North America, in Bering Sea drainages south to the Kuskokwim River, in the Yukon River to its headwaters in British Columbia, and in northern Bering Sea and in Arctic Ocean drainages as far east as Bathurst Inlet. Ascending the Mackenzie River to Camsell Bend at about 62°N. Not recorded from North American islands of the Bering Sea or Arctic Ocean except Herschel Island.

DISCUSSION

If two groups of fish occupy the same lake without interbreeding, and if every individual can be assigned to one or other group on morphological grounds, then the groups fulfill the usual criteria for two distinct species.

In this study it has been possible by combination of a pair of measurements with appropriate growth characteristics (e.g. gill raker length and interorbital width) to assign every specimen in each collection to one of two groups. The resultant grouping is consistent with that based on prior subjective assessment of the "general appearance" of each fish. Other combinations of measurements can be used to produce the same grouping. Moreover, for many meristic characters and proportional measurements the means differ markedly between the two groups, and differ in a consistent direction between pairs of groups from different localities.

No individual was found with intermediate characteristics and questionable identity; i.e., there were no apparent hybrids. Therefore, provided the morphological differences are genetic in origin, it may be taken as established that the two groups are not interbreeding and hence are distinct species.

Alternatively, the morphological differences might be entirely phenotypic, due to fish having developed under two different sets of environmental conditions. In this study, only collections were used which contained both types of fish from the same locality. Therefore it cannot be argued that some localities produce one type of fish and some the other, on a purely phenotypic basis. There could, however, be two types of environmental conditions present in *each* locality. Possible sources of duality are spring *versus* autumn spawning, shallow water *versus* deepwater spawning, or lake *versus* stream spawning. In order to produce two completely separable groups of phenotypes, there would have to be no overlap in the controlling environmental conditions at the two spawning sites. More importantly, there would have to be no overlap in such conditions

between one type of spawning site in *all* localities and the other type in *all* localities wherever the two groups of fish were produced. Complete dichotomy in the environment can be visualized in a single locality, but the requirement set forth above seems most unlikely to be met throughout the range of several thousand miles. Both types of fish have been examined from a wide variety of altitudes, climatic zones and types of water (clear lakes, clear or muddy rivers, tidal deltas). No environmental factor can be suggested which is sharply bimodal in distribution in every one of these localities and which has in no place a condition of intermediacy. Therefore, the perfect dichotomy of specimens, in all these localities *combined*, can scarcely have a purely phenotypic orgin.

There may very well be genetic differences between the two groups which cause each to select one extreme from an environmental gradient, and shun conditions of intermediacy. Under these circumstances, dichotomy in morphology of the young could conceivably have a purely phenotypic origin. But genetic discreteness in selection of spawning site fulfills the requirement for recognition of distinct species, so in this case the groups would qualify as two species even though their morphological differences were purely phenotypic.

Other hypotheses might be advanced, but the simplest and most probable interpretation of the data is that the broad whitefish *C. nasus* is a distinct and widespread species which can by appropriate means be clearly distinguished from all others.

Almost certainly *C. nasus* has distinctive habits as well as distinctive morphology separating it from "humpback" whitefishes. The shorter and usually less numerous gill rakers of the broad whitefish, and its distinctive mouth, suggest a diet somewhat different from that of the "humpbacks". Wynne-Edwards (1952) mentions an earlier upstream spawning migration of *C. nasus* than "humpbacks" in the Mackenzie River. Frequent sympatric occurrence of the two types of whitefish over a wide geographical area suggests some dividing up of niches between the two, but little is yet published on their ecology.

Despite suggestions of slight clines in some characters (e.g., in gill raker number in the Yukon River system) there are no geographic breaks in meristic characters of *C. nasus* in North America to warrant subspecific separation. Because of the inequality of specimen sizes in different samples little has been said here about geographic variation in morphometric characters. Body proportions certainly differ between some localities, but again there is no evidence of a geographic break justifying recognition of subspecies within North America. Neither do North American and Eurasian populations of *C. nasus* appear to differ subspecifically (Walters, 1955).

"Humpback" whitefish, on the contrary, although they have been lumped together here as a foil for *C. nasus*, show distinct evidence of subspecific or specific diversity. For example, gill raker counts of "humpbacks" may differ marbredly between different localities (Table II); the differences are probably not purely phenotypic, because broad whitefish from the same localities do not always show parallel divergence.

Evidence of parallel environmental influence on morphology of the two groups of fish is sparse. Geographic variation in characters of *C. nasus* does not closely parallel variation in "humpbacks", probably because the latter is actually a composite group. Relationships between "humpback" whitefish in northern Canada, Alaska and Eurasia have yet to be resolved.

ACKNOWLEDGMENTS

Each year from 1957 to 1961 Mr J. D. McPhail has accompanied me on collecting trips to northern Canada or Alaska, and has contributed in many ways to the present study. The acquisition of specimens and data from the Northwest Territories has depended largely on the generous cooperation of Mr J. G. Hunter of the Arctic Unit, Fisheries Research Board of Canada. Some specimens used were collected under harrowing conditions by field parties of the Arctic Unit during the 1959 survey of the Barren Grounds. Drs W. B. Scott and E. J. Crossman, who took part in the survey, have also provided specimens and have cooperated in other ways. Field measurements of specimens from Tuktoyaktuk and Anderson River were made by Mr M. E. Riske. Dr W. A. Clemens supplied measurements of Teslin Lake specimens. Whitefish from Coppermine village were collected by Dr D. V. Ellis, and those from Colville River by Dr E. B. Reed. Others who have contributed in various ways during collection of specimens are Dr S. Y. Coo, Mr Samuel J. Harbo Jr., Mr Don R. Miller, Prof. J. A. McLeod, Dr T. G. Northcote, Mr Dean Paddock, Dr Steven Pennoyer, Father Poole of St. Mary's Mission, Mr Ray Tremblay, Mr Gordon W. Watson and Dr W. C. Freihofer. Grateful acknowledgment is also made for a grant from the Arctic Institute of North America to collect fishes from Bering Sea drainages in 1960, and for grants from the University of British Columbia President's Committee on Research for collecting expeditions in 1958, 1960 and 1961. Dr N. J. Wilimovsky has provided useful criticisms of the manuscript; his knowledge of the literature on arctic fishes has been freely drawn on.

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ADDENDUM

Recent examination of two whitefish specimens in the United States National Museum (No. 60814), which are probably the basis for the Lake Bennett record of "*Prosopium kennicotti*" mentioned on page 707, shows them to be young humpback whitefish. The Lake Bennett locality for *C. nasus* should therefore be deleted from Fig. 1.

ANGLY

Effect of Food Quantity on Fecundity of Rainbow Trout, *Salmo gairdneri*[1]

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ABSTRACT

Studies of histology and development of rainbow trout ovaries indicate that the degree of follicular atresia is associated with degree of starvation during the maturation period. Experimental stocks raised under varying starvation regimes showed that the greater the starvation, the higher the proportion of maturing follicles which regressed. Thus the result was a lower number of eggs brought to maturity in starved fish.

Observations on natural populations indicate wide differences in egg size, with corresponding inverse differences in egg number at maturity. Egg size is apparently not effected by diet, but rather through natural selection depending on intraspecific competition. There appeared to be little correlation between egg size and fish size, but some difference did exist between age classes. Variations in egg number are therefore attributable to fish size, egg size and adequacy of diet. Starvation has also a lasting effect on the proportion of a given age-class which matures.

INTRODUCTION

The term "fecundity" usually refers to the numbers of mature eggs produced by a fish at spawning. As an important variable in population dynamics, fecundity variations, both within and between populations, merit serious investigation. Little experimental work on fecundity of fishes has been reported. Hayford and Embody (1931) described increased production of eggs in eastern brook trout, *Salvelinus fontinalis*, in the second and subsequent generations of fish selected for high growth rate and disease resistance. There was little data to suggest that this increase was the result of anything other than larger fish size at maturity.

Most studies of fecundity of fishes have been purely descriptive, chiefly from a taxonomic point of view. For example, several authors (McGregor, 1922, 1923a, 1923b; Gilbert and Rich, 1927; Foerster and Pritchard, 1936, 1941; Aro and Broadhead, 1950) have studied fecundity of Salmonidae as a means of separating races. Raitt (1932) described striking differences in fecundity between different age classes of North Sea haddock, *Melanogrammus aeglefinus*. Ricker (1932) and Raitt (1932) both established a logarithmic relationship between egg number and length of fish.

There have been many investigations of the endocrine functions of fish ovaries. Hoar (1955) has reviewed much of the pertinent literature in this field. Bretschneider and Duyvené de Wit (1947) have described formation of so-called

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corpora lutea in bitterling (*Rhodeus amarus*) and guppies (*Lebistes reticulatus*). Hoar (1955) suggested that pre-ovulatory *corpora lutea* are probably the main endocrine tissue of teleost ovaries. It seems safe to assume that trout ovaries have some endocrine function, but whether this is localized in regressing follicles is not known. Hoar does point out that as early as 1903, Wallace showed that, "whether or not *corpora lutea* are developed, resorption of ripening ova is a common feature in teleosts".

Differences in fecundity might arise between populations of a given species in two different ways. Svärdson (1949) postulated that interpopulation, intraspecific variations are the result of natural selection, on the one hand favouring those fish producing large numbers of small eggs each generation under conditions of little competition, but favouring fish producing larger and fewer eggs under conditions of high competition. Conversely, variations in fecundity might also arise from direct effects of environmental conditions on individual female fish.

In summarizing the literature, many physiological studies have been made of fish ovaries, a few mathematical presentations of fecundity variations have been made, and one work, that of Svärdson (1949), attempted to postulate a reason for these variations.

The present study was designed to assess some effects of semi-starvation on fecundity of rainbow trout, *Salmo gairdneri*. Facilities of the Smith's Falls (Cultus Lake) hatchery of the British Columbia Game Commission were used for the rearing of experimental stocks under varying diet regimes. The investigation was divided into three parts: (1) studies of histology and development of trout ovaries during the year of maturation, (2) rearing of trout under varying rations with analysis of fecundities of different groups at maturity, and (3) studies of fecundities of two natural populations of trout, from different, widely-separated lakes.

HISTOLOGY AND DEVELOPMENT OF TROUT OVARIES

Materials and Methods

Specimens of trout ovaries were collected from fish taken by anglers in Paul Lake, British Columbia, during 1951 and 1952. In addition, some maturing ovaries were taken from fish in the experimental stock. A representative series of these ovaries was fixed in 5% formalin, imbedded in paraffin to which 1% ceresin had been added, and sectioned both transversely and sagitally. The addition of ceresin facilitated sectioning of the yolky ova. The sections were stained in Heidenhain's Azan stain, which yielded brilliant contrast of the various tissues for photographic purposes.

General Structure and Histology

Trout ovaries consist of paired, trough-like structures lying parallel to the swim bladder. They are suspended by the *mesovaria*, attached to the mesal edges of the troughs, from the dorsal surface of the coelomic cavity. Partial transverse septa divide the troughs, and both septal and outside membranes bear follicles. Little interstitial tissue is present, the bulk of the organs being

made up of follicular tissue and ova. Figure 1 shows a transverse section of a trout body, indicating the relative placement of the organs.

Maturation of Trout Ovaries

Ovarian maturation in rainbow trout starts in early summer and is completed in the following spring. At the start of maturation, the ovaries are barely half the length of the swim bladder, and approximately 1/20 as wide. Gradually their bulk increases, until at spawning the ovaries occupy most of the coelomic cavity and may comprise 20% of the total mass of the specimen.

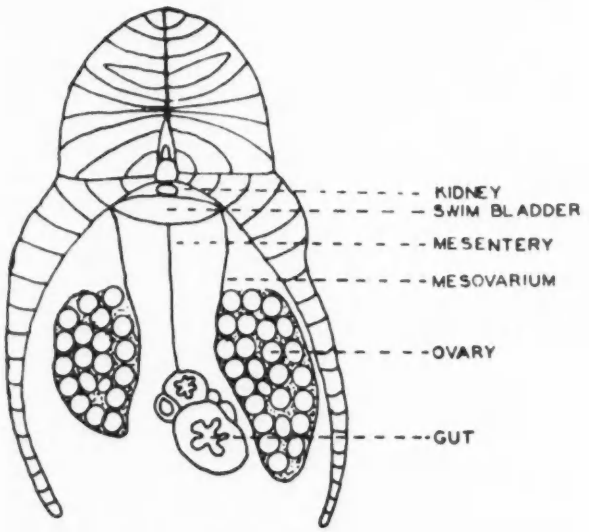


Fig. 1. Transverse section through body of rainbow trout at level of ovaries. Body cavity opened along mid-ventral line.

During maturation, three types of follicles are present. There are very small follicles containing ova without yolk and with a centrally-placed nucleus. These are resting follicles. The second type are the maturing follicles which, depending on the degree of maturation, may form the majority of the ovarian bulk. Finally, there are the so-called *corpora lutea* or *corpora atrectica*, as described by Bretschneider and Duyvené de Wit (1947). In these follicles a total resorption of the ova takes place, excepting in some cases, the egg membrane or *zona radiata*. Figures 2-7 show progressive changes in early, middle and late stage atresia of maturing follicles.

Mature Trout Ovaries

Some disparity in size between right and left ovaries usually exists in spawning trout. Occasionally, only one ovary is present, either right or left. At spawning, the follicles rupture, the eggs are shed into the space between lateral

body walls and ovary and travel back to be expelled through the genital orifice. From direct observation it can be seen that not all follicles rupture simultaneously; the eggs appear to be shed in groups starting from the posterior end of the ovary.

Endocrinology of Trout Ovaries

Direct examination of regressing trout ovarian follicles did not indicate that these are necessarily the sites of hormone formation. It is recognized (Hoar, 1955) that there is undoubtedly some endocrine function of trout ovaries, but whether the atretic follicles have anything to do with it is unknown. Whether or not they do in fact secrete hormones, the end result of follicular atresia is a reduction in the number of eggs brought to maturity. Regression of some follicles appears to be universal in all vertebrate females; in trout, some active resorption was taking place in every specimen examined. From this fact, two alternative or perhaps complementary hypotheses may be drawn:

1. regression of trout follicles is the result of the inability of the animal to produce more than a certain mass of follicular and oval material at a given time, necessitating the sacrifice of some follicles to permit others to grow, and/or

2. regression is a necessary precursor to the production by the granulosa cells of some hypothetical hormone, as demonstrated by Bretschneider and Duyvené de Wit (1947) for bitterling.

ARTIFICIAL INDUCTION OF FECUNDITY VARIATIONS IN RAINBOW TROUT

Materials and Methods

Five thousand yearling trout were reared at the Smith's Falls (Cultus Lake) hatchery of the British Columbia Game Commission under controlled feeding conditions for two years. The eggs from which these trout were reared came from Paul Lake, British Columbia. The trout were initially divided into two equal groups, and each group placed in one half of a concrete pond divided into inlet and outlet sections. The group in the inlet section was fed standard hatchery diet three days per week, whereas the group in the lower (outlet) end was fed every day. A summary of the amounts fed is contained in Appendix A; the composition of the food remained constant throughout the experiment.

During the first year (second year of growth) the groups were fed according to schedule from May 10 to August 15, 1953. Both groups were then allowed full diet until May 2, 1954, when the lower group were marked by removal of dorsal fins. The second year (third growth year) was divided into 4 periods: (1) May 2 to July 2, 1954, (2) July 2 to September 2, 1954, (3) September 2 to November 2, 1954, and (4) November 2, 1954 to May 2, 1955. At the beginning of each of the first 3 periods, half of each group was transferred to the opposite section, and at the end of the period, all fish which had been on full diet during the period were marked by removal of a fin. On November 2, 1954, the screen separating the two sections was removed and all specimens were placed on full diet for the remainder of the experiment. On May 2, 1955, all mature females

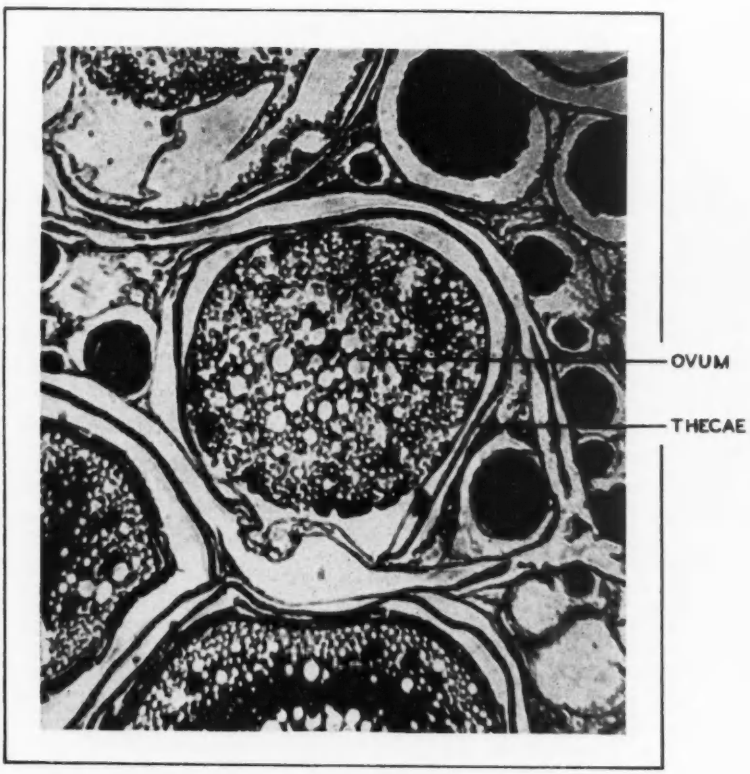


FIG. 2. Early stage regression of ovarian follicle in early maturation phase of rainbow trout (× 40). Note lack of *zona radiata* about ovum.

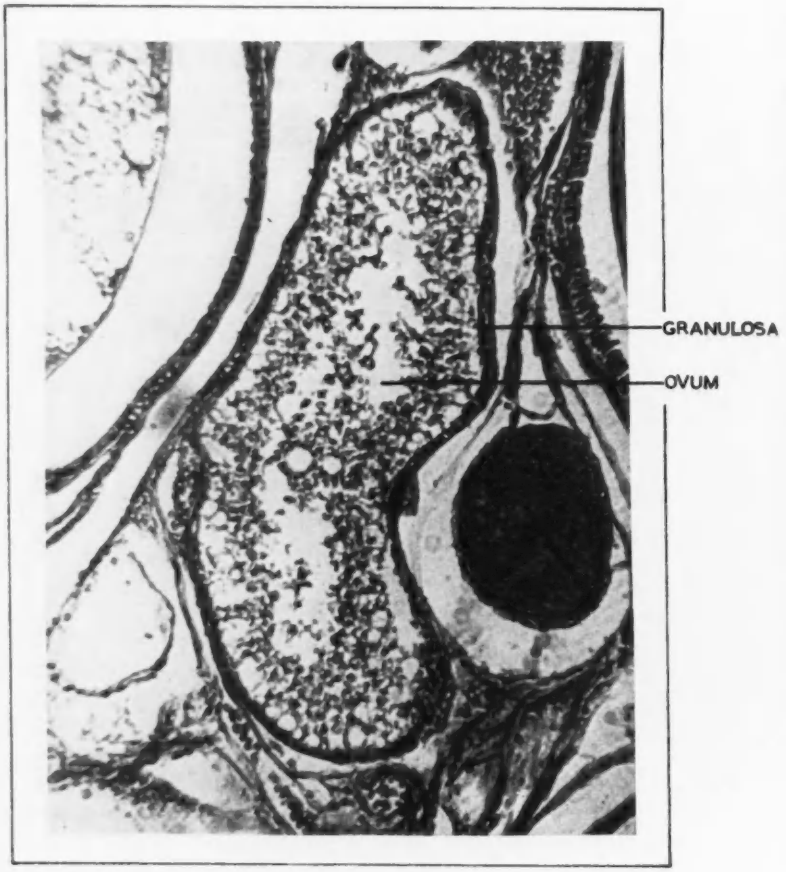


FIG. 3. Late stage regression of ovarian follicle in early maturation phase of rainbow trout (× 60).

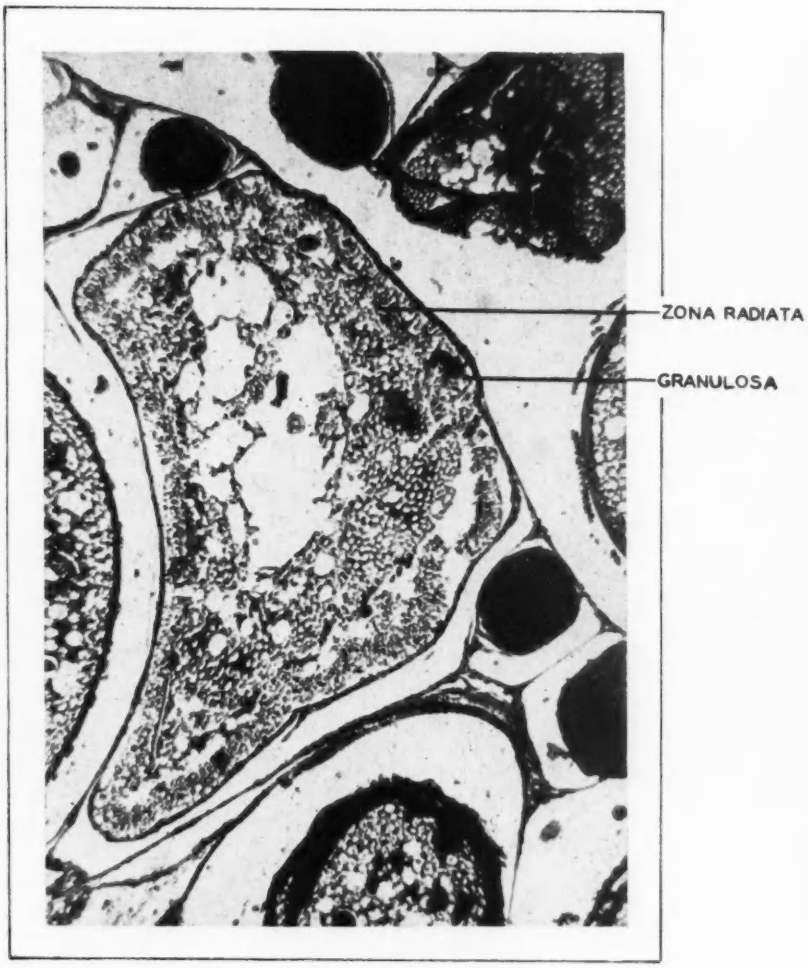


FIG. 4. Early stage regression of ovarian follicle in mid-maturation phase of rainbow trout (× 36). Note shrinkage and perforation of *zona radiata*.

FIG. 5. Late stage regression of ovarian follicle in mid-maturation phase of rainbow trout (× 50).

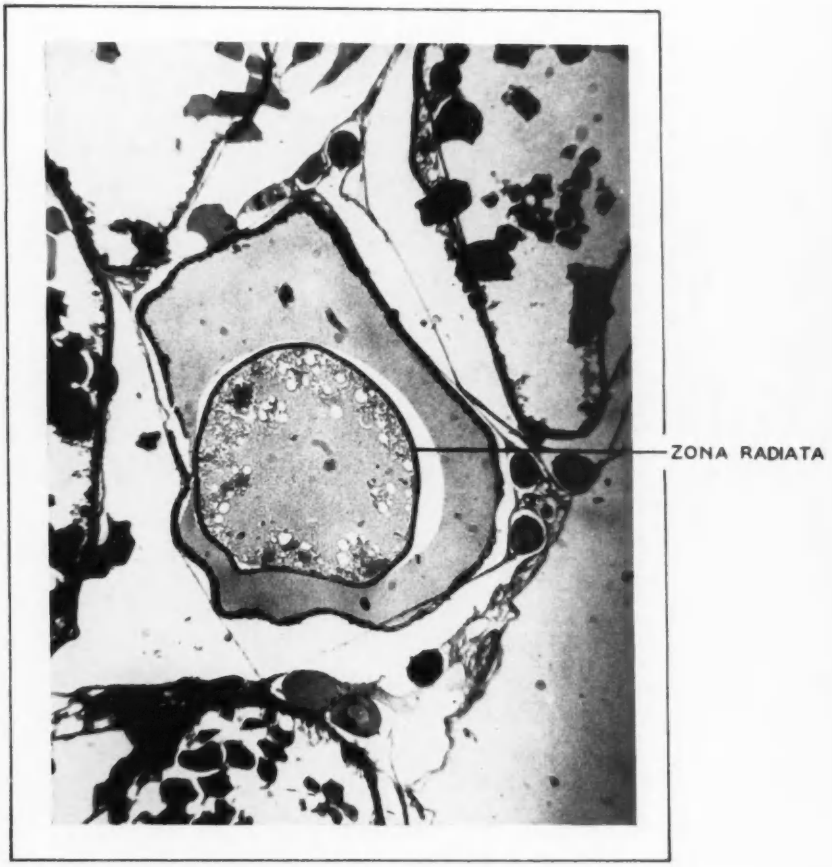


FIG. 6. Early stage regression of ovarian follicle in late maturation phase of rainbow trout (× 24). Note shrunken but imperforate *zona radiata*.

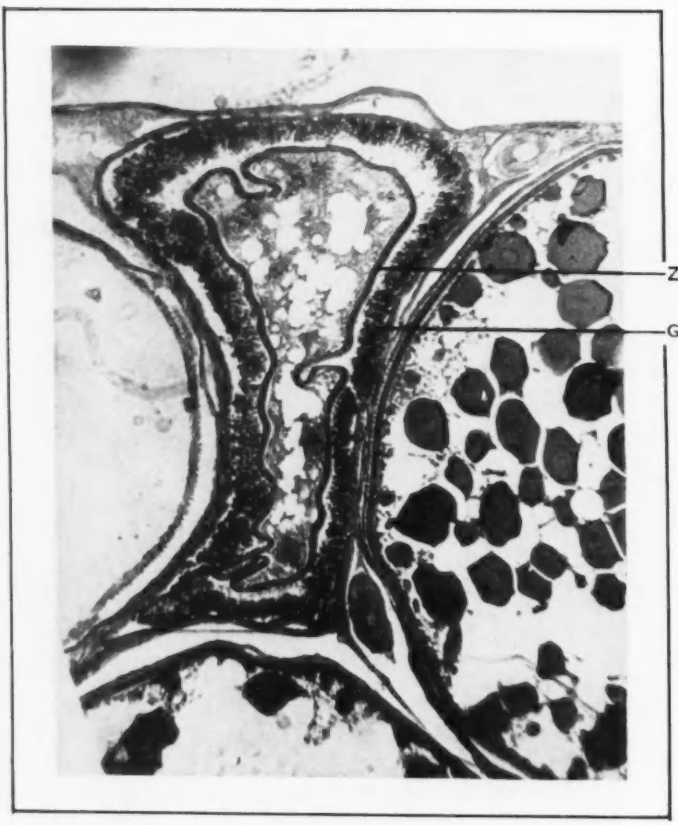
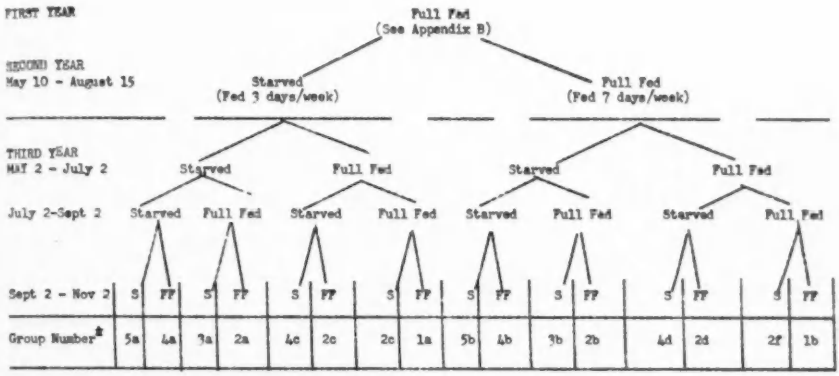


FIG. 7. Late stage regression of ovarian follicle in late maturation phase of rainbow trout (× 36). Note distortion of *zona radiata*.

were removed and preserved whole in 5% formalin. A sample of 30 trout was taken from each group at the end of each starvation period for study of the maturing ovaries.

The overall period, May 2 to November 2, covers approximately the first half of ovarian maturation in rainbow trout. Figure 8 presents the experimental plan.



*Referring to third year only:

Group 1. Full fed all three periods 1a + 1b = 8
Group 2. Starved one period 2a + 2b = 8, 2c + 2d = 4, 2e + 2f = 0 Total 12
Group 3. Starved for two periods separated by one full fed period 3a + 3b = 5
Group 4. Starved for two successive periods 4a + 4b = 5, 4c + 4d = 5 Total 10
Group 5. Starved for three periods 5a + 5b = 5

FIG. 8. Experimental plan for study of effect of level of diet on fecundity of rainbow trout.

RESULTS OF EXPERIMENTAL TREATMENT—SECOND YEAR STARVATION

Very few female trout in the experimental stock matured during their third year. Table I presents a chi-square analysis of relative frequencies of maturing and immature trout which were semi-starved or full fed during their second year. There can be little doubt that semi-starvation in the second year results in suppression of maturation in the third year. It appears also that the so-called

TABLE I. Chi-square analysis of relative proportions of rainbow trout of experimental stock starved or full fed during their second year which matured during their third year. Figures in parentheses indicate expected values.

	Starved	Full fed	Total
Mature	20 (46.4)	57 (30.6)	77
Immature	955 (928.6)	586 (612.4)	1541
Total	975	643	1618

Chi-square = 39.69 ($P<0.0001$)

full diet, combined with hatchery conditions, was inadequate since only 9% matured, whereas Larkin *et al.* (1950) showed that, in nature, the same stock (Paul Lake, B.C.) shows 60–70% of females maturing in their third year.

Results of Experimental Treatment—Ovaries from Maturing Trout

Few maturing specimens were found in the samples taken at the end of each starvation period. In all, 17 specimens were taken at the end of starvation period 3, the sampling preceding the final period of experimental starvation. Counts of maturing and regressing follicles were made on the ovaries, and the data grouped according to the severity of diet restriction. Table II presents the results in the form of a regression analysis, where the group number is used as an arbitrary independent variable. A highly significant regression exists with negative slope, indicating that the worse the starvation, the lower the ratio between maturing and regressing follicles. In other words, a higher proportion of maturing follicles undergo atresia, the greater the diet restriction.

Table II. Regression analysis of proportion of maturing and regressing follicles in rainbow trout ovaries from experimental stock taken at end of starvation period. X = $\log_{10}$(group number); Y = $\log_{10}$(ratio of maturing to regressing follicles). Group numbers: *1* = no starvation period; *2* = one starvation period; *3* = two starvation periods separated; *4* = two consecutive starvation periods; *5* = three starvation periods.

Statistic	Symbol	Value
Number of specimens	n	17.
Average X	$\overline{X}$	0.3274
Average Y	$\overline{Y}$	0.5617
Regression coefficient	b	−1.4393
Standard error of b	...	0.3571
Correlation coefficient	r	−0.721
Probability of significance	P	<0.001

Results of Experimental Treatment—Mature Ovaries

Only 40 mature female trout were obtained from the experimental stock; these were derived from 12 of the 16 diet groups, as shown in Fig. 8.

Measurements were made on each specimen of the following variables:

1. fork length (cm);
2. net weight (g), that is, total weight minus total weight of eggs;
3. total number of mature eggs;
4. egg size (g); the size was expressed as the average weight of an individual egg. It was determined by weighing 100 or more eggs and dividing by the egg number in the sample. The data were amalgamated into 5 groups, according to the severity of diet restriction, as in the previous section. All computations were performed on logarithmic data, since the mathematical relationships between these variables are well established (Ricker, 1932; Raitt, 1932).

Three between-groups comparisons were made. These were:

1. average size of egg between groups;
2. net weight *on* fork length between groups;
3. egg number *on* fork length and average size of egg.

Each comparison was tested for differences in adjusted group means, group slopes (where applicable) and group variances. Table III presents the pertinent statistics used, and Table IV presents the results of the analyses of variance and covariance, and test for homogeneity of variance.

TABLE III. Table of statistics for between-groups comparisons of fecundity variations in experimentally-reared rainbow trout. Probability levels: * denotes $0.05 \geqq P > 0.01$; ** denotes $P \leqq 0.01$. Symbols used are as follows: $X_1 = \log_{10}$(average weight per egg, in grams); $X_2 = \log_{10}$(egg number); $X_3 = \log_{10}$(fork length in cm); $X_4 = \log_{10}$(net weight in grams—i.e., total weight less weight of eggs).

Statistic	Symbol	Age group 1	2	3	4	5	Total
Number of specimens	n	8	12	5	10	5	40
Means of variates	$\overline{X}_1$	−1.29165	−1.27412	−1.27162	−1.27975	−1.27183	−1.27843
	$\overline{X}_2$	2.80221	2.80049	2.88630	2.63646	2.57451	2.74230
	$\overline{X}_3$	1.37629	1.40344	1.42109	1.38385	1.36287	1.39024
	$\overline{X}_4$	2.18326	2.26462	2.33586	2.21082	2.16412	2.23093
Sums of squares of deviations	Sx_1^2	0.010723	0.016638	0.015311	0.016187	0.018709	0.079655
	Sx_2^2	0.294255	0.214302	0.047270	0.191819	0.174025	1.347492
	Sx_3^2	0.028263	0.016301	0.016380	0.028480	0.017366	0.119351
	Sx_4^2	0.251587	0.134320	0.141945	0.243831	0.165182	1.049285
Simple correlation coefficients	r_{12}	−0.361	+0.068	+0.052	−0.317	−0.825	−0.251
	r_{13}	−0.186	+0.257	+0.217	+0.117	+0.586	−0.064
	r_{14}	−0.197	+0.268	+0.188	−0.171	−0.499	−0.065
	r_{23}	+0.967**	+0.727**	+0.961**	+0.861**	+0.934*	+0.817**
	r_{24}	+0.977**	+0.752**	+0.960**	+0.873**	+0.895*	+0.812**
	r_{34}	+0.995**	+0.975**	+0.997**	+0.993**	+0.994**	+0.991**
Multiple correlation coefficients	$R_{1.23}$	0.740	0.298	0.608	0.442	0.976*	0.351
	$R_{2.13}$	0.984**	0.738*	0.975*	0.888**	0.995**	0.841**

Examination of the tabulated data yields a number of conclusions:

1. No significant regression of egg size *on* fish size is demonstrated. Egg size may therefore be compared directly between groups.

2. No significant between-groups differences in egg size is demonstrated.

3. Highly significant differences in adjusted group mean egg number exists in the between-groups comparison of egg number *on* fork length and average egg size. (The addition of egg size to the simple regression of egg number *on* fork length results in a significant reduction in residual error variance.) In

TABLE IV. Analyses of variance and covariance and tests for homogeneity of variance for between-groups comparisons of variations in fecundity in experimentally-reared rainbow trout. "F" and chi-square values given with degrees of freedom in parentheses. For methods, see Snedecor (1946). Asterisks as in Table III.

	Variate relationship				Bartlett's test of homogeneity of group variances	
	Homogeneity of group means		Homogeneity of group slopes			
	F	*d.f.*	F	*d.f.*	χ^2	*d.f.*
Group average weight/egg	0.236	(4, 35)	...	...	3.273	(4)
Net weight *on* fork length	1.490	(4, 34)	0.361	(4, 30)	3.714	(4)
Egg number *on* fork lengths and average weight per egg	9.379**	(4, 33)	0.731	(8, 25)	4.781	(4)

other words, although egg *size* is apparently not affected by diet restriction, egg *number* at maturity is reduced.

4. No significant differences are shown in the relation of net weight to fork lenght between groups; diet restriction therefore appears to have little or no lasting effect on physical condition.

5. No differences in regression slopes are apparent in the foregoing comparisons of net weight on fork length, and egg number on fork length, indicating that no differential effect of diet restriction on small or large fish was detected.

6. No significant differences in variances are apparent between groups for any of the variates, indicating that starvation has little effect on variability, regardless of its severity.

SUMMARY OF EXPERIMENTAL RESULTS

From the foregoing results, one may postulate that some factor other than size of fish or diet restriction predetermines egg size, and, other things being equal, egg number is a direct function of size of fish and size of eggs. The results strongly indicate that starvation reduces the number of eggs brought to maturity through the mechanism of follicular atresia. It should be noted that all specimens used were within a narrow range of length and belonged to the same age — and year-class of a single population. It is possible that egg size differences might be found if either different age-classes were compared, or if a wide range of lengths could be compared within a single age and year-class. Finally, diet restriction appears to result in lowered maturation rate, there being an apparent prolonged effect. Either inadequate food quantity was provided even for the full-fed trout or some essential food element was insufficient for their dietary needs.

FECUNDITY VARIATIONS IN NATURAL POPULATIONS

The study of natural populations was divided into 4 parts: (1) seasonal changes in weigth-length relationship of trout in Paul Lake; (2) seasonal changes in stomach content volumes of trout in Paul Lake; (3) examination of maturing ovaries from trout in Paul Lake during the first half of maturation; and (4) comparisons of fecundities of trout from Paul and Pennask Lakes at maturity.

Materials and Methods

Lengths, weights, scale samples, ovaries and stomachs were taken of 646 rainbow trout taken by anglers in Paul Lake, 1952. A large sample of spawning female trout was taken from the Paul Creek (inlet to Paul Lake) fish trap in May, 1952 for studies of fecundity. Another large sample was taken from the Pennask Creek (inlet to Pennask Lake) fish trap in July, 1951. Both samples of spawners were preserved whole in 5% commercial formalin. After full preservation, fork length, net weight, egg size and egg number were recorded for each specimen, and the age and spawning history were determined from the scales of each fish. Care was taken to use only fish which were fully ripe, the criterion being that there were at least 2 but less than 20 ruptured follicles. Comparisons were made entirely on logarithmic data, and followed the pattern of analysis used in the study of the experimental stock.

Description of Natural Stocks

Paul Lake has had a population of rainbow trout for only about 50 years, prior to which it was barren of fish. The population was established by stocking with fry from Adams Lake trout (Larkin *et al.*, 1950). Since that time, as well as before, the stock has been entirely cut off from immigration by natural barriers. From the few records available, the lake has never been highly populated, partly because of somewhat limited spawning grounds and partly due to heavy angling pressure.

Pennask Lake, on the other hand, has probably had rainbow trout in it for centuries. Local Indian legends tell of expeditions each spring to the lake to collect spawning trout for food. Only the one species occupies the lake. In contrast to the population of Paul Lake, the Pennask Lake trout population is exceedingly large, and the growth is somewhat depressed for this reason. Some indication of the enormous numbers of trout may be obtained from the fact that personnel at the Pennask Lake hatchery have been able to take as many as 6 million eggs on many occasions from the spawning fish, necessitating the handling of at least 6000 female trout and a roughly corresponding number of males. There was no reason to believe on these occasions that the supply was overtaxed. No immigration of trout to the lake is possible due to natural barriers.

Weight–Length Relationships of Paul Lake Rainbow Trout

The weights and lengths of 349 female trout taken by anglers in Paul Lake in 1952 were grouped into 10 two-week periods for comparisons. Table V presents the pertinent statistics and analysis of covariance for between-groups comparisons of the seasonal groups. Although highly significant differences in adjusted group means and variances exist, there is no apparent pattern to these changes. The results perhaps indicate a seasonal change, although tests indicate that chronologically adjacent samples do not in general show significant differences. The overall regression slope of 3.021 indicates isogeny of the weight-length relationship in the population as a whole.

TABLE V. Analysis of covariance for between-groups comparisons of the relationship of log weight to log length in female rainbow trout taken by anglers in Paul Lake, 1952. Asterisks as in Table III. $X = \log_{10}$ (fork length in cm); $Y = \log_{10}$ (weight in grams, not including eggs).

Seasonal group	Number in sample	Means of variates		Sums of squares of deviations		slope coefficient	Correlation coefficient
		$\overline{X}$	$\overline{Y}$	Sx^2	Sy^2	b	
May 18–31	74	1.4708	2.4134	0.198522	1.994424	3.075	+0.970**
Jun. 1–14	91	1.4947	2.5057	0.193930	1.715756	2.880	+0.968**
Jun. 15–28	55	1.4851	2.4615	0.151678	1.423624	2.938	+0.959**
Jun. 29–Jul. 12	15	1.5174	2.5571	0.027373	0.267457	3.040	+0.973**
Jul. 13-26	19	1.4650	2.4344	0.068891	0.733334	3.197	+0.980**
Jul. 27–Aug. 9	20	1.4930	2.4950	0.045037	0.532873	3.336	+0.970**
Aug. 10–Aug. 23	19	1.5035	2.5575	0.130138	1.167883	2.913	+0.972**
Aug. 24–Sept. 6	16	1.4883	2.4951	0.080363	0.690791	2.716	+0.926**
Sept. 7–Sept. 20	25	1.4946	2.5173	0.158677	1.537908	3.098	+0.995**
Sept. 21–Oct. 4	15	1.4820	2.4652	0.087751	0.860700	3.116	+0.995**
Total	349	1.4870	2.4783	1.198088	11.620364	3.021	+0.970**

Test	F	*d.f.*	Chi-square	*d.f.*
Homogeneity of adjusted group means	3.961**	(9, 338)	...	...
Homogeneity of group slopes	1.368	(9, 329)	...	...
Homogeneity of group variances	...	...	60.177**	(9)

STOMACH CONTENT VOLUMES OF PAUL LAKE RAINBOW TROUT

The volumes of stomach contents from 646 anglers' catch specimens were corrected for differences in fish size by means of the following equation:

$$\text{corrected volume} = \text{actual volume} \times \left(\frac{30.0}{\text{fork length}}\right)^3$$

The correction gives a figure which is a measure of stomach fullness, assuming that normal "full" stomach volume should vary roughly as the cube of the length and that a length of 30 cm is an appropriate "standard". It would otherwise be necessary to analyse the data in regression form.

The data were transformed into logarithms to correct for correlated mean and variance in the original arithmetic data. The mean corrected volumes are presented in Fig. 9 in arithmetic retransformation, together with the resultant asymmetric 95% confidence limits. Mean values are therefore geometric means.

Figure 9 shows that there is a very sharp decrease in stomach fullness between May 18 and June 15, coinciding with the spring warming of the lake. For the rest of the period, no significant trend is obvious. The mean value for the latter period is just over 1.0 ml, a very small quantity for a 30.0 cm fish. Although trout are known to regurgitate some of their food when caught, it seems unlikely that there would be any major seasonal change of this phenomenon. Likewise, the rate of digestion, although probably higher at the higher summer temperatures, seems unlikely to account for quite such large differences as shown in Fig. 9.

Since ovarian maturation appears to commence between May 15 and July 1 in rainbow trout, most of the fish are apparently under conditions of lowered food intake during the first 3 to 4 months of maturation.

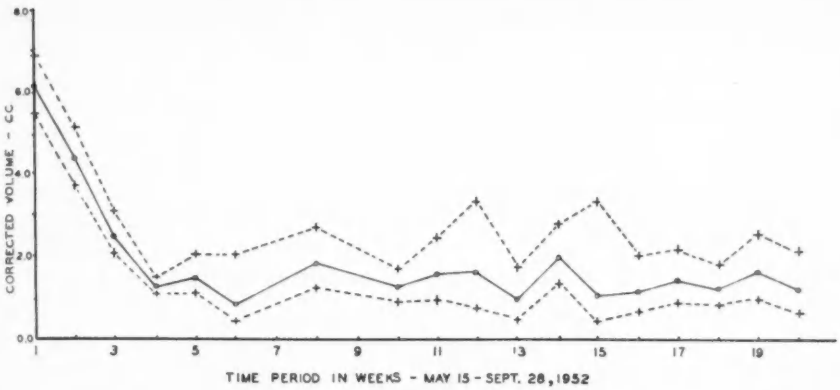


FIG. 9. Mean corrected stomach content volumes in millilitres, with 5% confidence limits, of rainbow trout taken by anglers in Paul Lake, 1952. Disproportionate limits determined from logarithmic transformation.

MATURING OVARIES FROM PAUL LAKE RAINBOW TROUT

Thirty-two pairs of ovaries taken from trout caught by anglers in Paul Lake between May 15 and September 15, 1951 were studied. These were weighed, a sample of eggs weighed and the eggs in the sample counted and measured. Measurement was made by means of an ocular micrometer; egg diameters were expressed in units equal to 0.1823 mm. The results are shown in Table VI; ovaries were classified on the basis of modal frequencies of egg diameter. To correct roughly for fish size, egg number variations are expressed as number of eggs per gram of fish.

Table VI shows an apparent sharp decrease in number of eggs per gram of fish when modal diameter is between 10 and 11 units. Since all eggs were counted, this is simply the point at which the steadily shrinking regressive follicles

TABLE VI. Frequency distributions of egg diameters from ovaries taken by anglers in Paul Lake between May 15 and Sept. 15, 1951. Data are grouped according to modal classes. One egg diameter unit = 0.1823 millimetre.

Egg diameter modal class in units	Number of ovaries	Egg diameter in units																		Eggs per gram of fish
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	
6.0–.9	4	2	32	28	19	48	**199**	80	5	...	...	...	...	...	...	...	...	...	...	12.655
7.0–.9	8	...	1	19	17	51	185	**429**	179	8	...	...	...	...	...	...	...	...	...	9.288
8.0–.9	5	...	...	7	26	55	71	144	**241**	91	5	...	...	...	...	...	...	...	...	9.737
9.0–.9	3	...	...	6	10	8	9	26	44	**147**	69	24	8	1	...	...	...	...	...	8.901
10.0–.9	2	...	...	...	5	2	5	4	8	35	**67**	57	16	1	...	...	...	...	...	8.414
11.0–.9	1	...	...	1	1	1	...	1	4	7	31	**46**	26	2	...	...	...	...	...	3.941
12.0–.9	4	...	...	1	4	1	...	1	1	3	22	74	**163**	102	26	2	...	...	...	5.008
13.0–.9	1	...	...	...	1	...	1	1	1	2	4	3	7	**36**	31	8	4	1	...	4.667
14.0–.9	2	...	...	...	2	...	...	...	...	1	...	1	8	38	**90**	53	8	...	...	4.424
15.0–.9	0	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
16.0–.9	1	...	...	...	...	...	...	...	...	...	...	1	1	1	3	24	**41**	27	2	2.523
17.0–.9	1	...	...	1	2	...	...	1	...	...	...	...	...	1	2	16	26	**31**	20	3.870

reach the visibility limit at the magnification used. The table indicates, however, that as their size increases, the numbers of *viable* eggs diminish in these trout. From studies of mature Paul Lake trout, it was found that the average number of eggs per gram of fish at maturity was 4.079 for 3-year-old first spawners and 4.418 for 4-year-old second spawners. Hence, during the summer period prior to spawning, the number of eggs is reduced to the number which will eventually be spawned.

While the cause and effect relationship between low stomach content volume and follicular atresia cannot be demonstrated, there is strong circumstantial evidence, both from the experimental work and the Paul Lake maturing fish, that this is indeed the case.

Mature Ovaries from Paul Lake and Pennask Lake Rainbow Trout

Ovaries from 48 Paul Lake rainbow trout and 50 Pennask Lake rainbow trout were used for between-groups comparisons of fecundity. Two age groups were involved in each lake, 3-year-olds spawning for the first time (IIIs), and 4-year-olds spawning for the second time (IIIs-IVs). The analyses were carried out for group comparisons as in the experimental section. Table VII presents the pertinent statistics, and Table VIII gives the results of between-groups comparisons.

From examination of these tabulated data, several conclusions may be drawn. These are:

1. Within groups, there is little relationship between egg size and fish size, as was shown in the experimental fish.

2. Whereas no significant difference is shown in egg size between the two age classes of Paul Lake fish, a significant difference does exist in Pennask Lake rainbow trout, those of the IIIs-IVs fish being larger than those of the IIIs specimens.

3. In the between ages comparisons, significant differences in adjusted group means exist within each lake, but not between lakes in the net weight-fork length relationship. No significant differences are apparent in slopes or variances.

4. Highly significant differences exist in egg sizes between lakes within age classes in means but not in variances.

5. Highly significant differences exist in the relationships of egg number *on* fork length and egg size between lakes within age classes in adjusted group means. In IIIs fish, differences between lakes also exist in regression slope and variance.

6. Pennask Lake trout show age-class differences in adjusted group means in the multiple regression, while Paul Lake trout only show a difference in variance.

It should be noted that the totals columns are included in Table VII only for convenience. It can be seen by inspection that there is a high degree of interaction between egg size and lake of origin in the relationship of egg size on fork length (r_{13} and r_{14}) in that, whereas these correlations are predominantly positive or slightly negative within subsamples, the grand total gives highly

TABLE VII. Table of statistics for between-groups comparisons of fecundity variations in natural rainbow trout populations. See page 726 for definitions of groups. Asterisks and symbols are as in Table III.

	Group						
	Paul Lake			Pennask Lake			
Statistic	IIIs	IIIs-IVs	Total	IIIs	IIIs-IVs	Total	Total
Number of specimens	18	30	48	23	27	50	98
Means of variates							
$\overline{X}_1$	−1.39438	−1.42254	−1.41198	−1.24985	−1.20007	−1.22297	−1.31555
$\overline{X}_2$	3.13830	3.39876	3.30109	2.66016	2.73297	2.69948	2.99414
$\overline{X}_3$	1.49318	1.56479	1.53794	1.41913	1.45520	1.43861	1.48726
$\overline{X}_4$	2.44430	2.67545	2.58877	2.22350	2.34178	2.28737	2.43499
Sums of squares of deviations from means							
Sx_1^2	0.076455	0.206099	0.291474	0.094240	0.055474	0.180492	1.346883
Sx_2^2	0.695967	0.668378	2.127514	0.079712	0.273712	0.419275	11.410383
Sx_3^2	0.041747	0.053369	0.152809	0.009417	0.013943	0.039523	0.433940
Sx_4^2	0.370819	0.477578	1.449451	0.083704	0.130434	0.387869	4.061991
Simple correlation coefficients							
r_{12}	−0.377	−0.189	−0.304*	−0.168	−0.086	+0.228*	−0.766**
r_{13}	−0.001	+0.252	+0.018	+0.487*	+0.058	+0.455**	0.546**
r_{14}	−0.064	+0.266	−0.546	+0.421*	+0.158	+0.468**	−0.542**
r_{23}	+0.789**	+0.820**	+0.875	+0.280	+0.688**	+0.643**	+0.919**
r_{24}	+0.814**	+0.772**	+0.869**	+0.234	+0.699**	+0.645**	+0.914**
r_{34}	+0.976**	+0.973**	+0.983**	+0.874**	+0.932**	+0.947**	+0.989**
Multiple correlation coefficients							
$R_{1.23}$	0.611*	0.736**	0.660**	0.581*	0.183	0.463**	0.865**
$R_{2.13}$	0.873**	0.917**	0.931**	0.447	0.699**	0.647**	0.972**

negative results. The overriding effect of small Pennask Lake trout with large eggs compared with larger Paul Lake trout with small eggs leads to spurious conclusions if only the totals column is examined.

SUMMARY OF STUDY OF NATURAL POPULATIONS

To summarize, there is evidence from the study of stomach contents, maturing ovaries and weight-length relationships from Paul Lake rainbow trout that some diet restriction exists in this lake during the summer, coincident with follicular atresia. Studies of mature trout from Paul and Pennask Lakes indicate that very real differences exist in the fecundities of these trout populations. Pennask Lake trout produce few large eggs, whereas Paul Lake fish produce many more but smaller eggs. There is no strong evidence of age-class differences in Paul Lake, but the two age-classes of Pennask Lake trout show strong differences.

TABLE VIII. Analyses of variance and covariance, and test for homogeneity of variance for between-groups comparisons of fecundity variations in natural populations shown in Table VII. "F" ratios are given, with degrees of freedom in parentheses. Asterisks as in Table III. Tests are as follows: A = F-test for homogeneity of adjusted group means; B = F-test for homogeneity of group slopes (where applicable); C = F-test for homogeneity of group variances (variance ratio).

Group	Test	Variates: Group average weight per egg	Net weight *on* fork length	Egg number *on* fork length and av. weight per egg
Paul IIIs vs	A	1.452 (1, 46)	3.802 (1, 45)*	0.298 (1, 44)
Paul IIIs–IVs	B	...	0.000 (1, 44)	0.294 (2, 42)
	C	1.580 (17, 29)	1.209 (16, 28)	2.776 (15, 27)*
Pennask IIIs vs	A	9.868 (1, 48)**	3.349 (1, 47)*	4.970 (1, 46)*
Pennask IIIs–IVs	B	...	0.420 (1, 46)	1.750 (2, 44)
	C	2.007 (22, 26)	1.378 (21, 25)	1.828 (24, 20)
Paul IIIs vs	A	49.193 (1, 39)**	0.442 (1, 38)	7.091 (1, 37)**
Pennask IIIs	B	...	0.664 (1, 37)	2.501 (2, 35)*
	C	1.050 (17, 21)	1.162 (16, 21)	3.448 (15, 20)**
Paul IIIs–IVs vs	A	149.886 (1, 55)**	1.308 (1, 54)	11.165 (1, 53)**
Pennask IIIs-IVs	B	...	1.442 (1, 53)	1.073 (2, 51)
	C	3.330 (29, 26)	1.268 (28, 25)	1.471 (24, 27)

SUMMARY AND DISCUSSION

Briefly stated, the results of these investigations have been as follows:

Follicular regression (atresia) has been shown to be a phenomenon which lowers the numbers of maturing eggs in rainbow trout. It is not known whether this is a simple sacrifice, because only a limited number can be produced, or if hormone production from the atretic follicles is a part of the physiology of maturation.

Experimental diet restriction, in addition to delaying maturity, can influence egg number by increasing the rate of follicular atresia. Increasing restriction of food intake increases follicular atresia, but does not apparently influence the size of eggs at maturity. Egg size is apparently determined by some factor other than size of fish or starvation within a particular age class and year class, perhaps genetically. The addition of egg size significantly improves the mathematical relationship between egg number and fork length; if the eggs are larger, then the number produced at maturity is smaller.

In a natural population (Paul Lake), the reduction in number of eggs caused by follicular regression occurs in the summer months coincident with a decrease in stomach content volumes. A condition of semi-starvation may be postulated, although changes in weight–length relationship did not follow a similar seasonal pattern.

Comparisons of spawners from two age-classes from Paul Lake showed little significant difference in egg size, weight–length relationship, or the multiple regression of egg number *on* fork length and egg size. In Pennask Lake, the

4-year-old second spawners produced larger eggs than the 3-year-olds. Both age groups from Pennask Lake produced bigger eggs and fewer eggs than the corresponding age groups from Paul Lake. The Pennask Lake fish also produced a smaller total egg mass. None of these differences was associated with any difference in weight–length relationships.

From the foregoing it would appear that follicular atresia may be a factor in the dynamics of trout populations. Increases in the intensity of intraspecific competition would cause reduction in egg numbers commensurate with the degree of starvation.

Natural selection for larger egg size might also occur in many ways under conditions of intense intraspecific competition (Svärdson, 1949). It is known that rainbow trout show agressive behaviour and form size-influenced social hierarchies as underyearlings (Stringer and Hoar, 1955). Larger egg size thus would have a selective value in highly competitive situations. This would appear to be the explanation for the differences between Paul and Pennask Lake trout populations. In the latter, competition is more intense, the number of eggs is smaller, and on the average they are larger. It may be supposed that fish which have begun life as larger eggs will be more robust and for this reason will be disproportionately represented in the second spawner group.

It may be that with further study of the effects of intraspecific competition on fecundity, it would be possible to use these relationships as indices of relative density of trout populations. The method might also be extended to the use of fecundity measures as indices of environmental conditions for anadromous species. It has been shown that there are differing egg numbers per unit fish size in several species of Pacific salmon (McGregor, 1922, 1923a, 1923b; Foerster and Pritchard, 1941; Aro and Broadhead, 1950). The relationship of egg number and egg size has not been extensively studied. Changes in egg size for a particular race might be an indicator of conditions of existence in the freshwater environments; similar differences between races might show the same. Differences in egg number from year to year probably indicate differences in marine conditions. Differences in egg number between races beyond those associated with differences in marine conditions may be associated with selection for the maximum egg load in relation to the distance which must be traversed to the racial spawning area, or differences in spawning ground conditions.

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Appendix A

Production diet used at Smith's Falls hatchery. Pork liver 45%, salmon viscera 45%, pork spleen 10% plus 2 lb salt per 100 lb feed; 3% brewer's yeast added twice or 3 times per week. The table below indicates the number of pounds of food per 100 lb of fish per day.

Water temp. (F)	Approximate size in inches (1 inch = 2.54 cm)										
	–1	1–2	2–3	3–4	4–5	5–6	6–7	7–8	8–9	9–10	10–
36	5.3	4.4	3.5	2.6	2.0	1.6	1.3	1.1	1.0	0.9	0.8
37	5.5	4.6	3.7	2.8	2.1	1.7	1.4	1.2	1.0	0.9	0.8
38	5.8	4.8	3.9	2.9	2.2	1.7	1.4	1.2	1.1	1.0	0.9
39	6.0	5.0	4.0	3.0	2.3	1.8	1.5	1.3	1.1	1.0	0.9
40	6.3	5.2	4.2	3.1	2.4	1.9	1.6	1.4	1.2	1.0	1.0
41	6.6	5.5	4.4	3.3	2.5	2.0	1.7	1.4	1.2	1.1	1.0
42	6.9	5.7	4.6	3.5	2.6	2.1	1.7	1.5	1.3	1.1	1.0
43	7.2	6.0	4.8	3.6	2.7	2.2	1.8	1.5	1.4	1.2	1.1
44	7.5	6.2	5.0	3.8	2.8	2.3	1.9	1.6	1.4	1.3	1.1
45	7.9	6.5	5.3	4.0	3.0	2.4	2.0	1.7	1.5	1.3	1.2
46	8.2	6.7	5.5	4.1	3.1	2.5	2.1	1.8	1.5	1.4	1.2
47	8.6	7.1	5.8	4.3	3.2	2.6	2.2	1.8	1.6	1.4	1.3
48	9.0	7.5	6.0	4.5	3.4	2.7	2.3	1.9	1.7	1.5	1.3
49	9.4	7.8	6.3	4.7	3.5	2.8	2.4	2.0	1.8	1.5	1.4
50	9.9	8.1	6.5	4.9	3.7	2.9	2.5	2.1	1.9	1.6	1.5
51	10.3	8.5	6.8	5.1	3.8	3.1	2.6	2.2	1.9	1.7	1.5
52	10.7	8.9	7.1	5.3	4.0	3.2	2.7	2.3	2.0	1.8	1.6
53	11.2	9.3	7.5	5.6	4.2	3.4	2.8	2.4	2.1	1.9	1.7
54	11.6	9.7	7.8	5.8	4.4	3.5	2.9	2.5	2.2	1.9	1.8
55	12.2	10.1	8.2	6.1	4.6	3.7	3.0	2.6	2.3	2.0	1.8
56	12.7	10.5	8.5	6.4	4.8	3.8	3.2	2.7	2.4	2.1	1.9
57	13.4	11.0	8.9	6.7	5.0	4.0	3.3	2.8	2.5	2.2	2.0
58	14.0	11.5	9.3	6.9	5.2	4.2	3.5	3.0	2.6	2.3	2.1
59	14.5	12.0	9.7	7.2	5.4	4.4	3.6	3.1	2.7	2.4	2.2
60	15.1	12.6	10.1	7.6	5.7	4.6	3.8	3.2	2.8	2.5	2.3

NOTES

The Phospholipid Content of Lingcod Muscle During Frozen Storage

Investigations by Dyer and Fraser (1959), Olley and Lovern (1960) and Bligh (1961) have established that phospholipid is degraded in the muscle of Atlantic cod (*Gadus callarias*) during frozen storage. Recently Wood and Haqq (1962) have demonstrated the formation of free fatty acid, presumably in part from phospholipid, in the muscle of frozen lingcod (*Ophiodon elongatus*). In view of this latter finding, and of the fact that Tomlinson *et al.* (1960) found no statistically significant loss of phosphorus from the phospholipid fraction of iced lingcod muscle, whereas Lovern *et al.* (1959) found such a loss in iced Atlantic cod (although the rate of loss was very low during the first 2 weeks), it seemed desirable to examine the phospholipid of lingcod muscle during frozen storage.

Lingcod were killed by a blow on the head, lateral-dorsal muscle was removed at once, frozen in liquid nitrogen, placed in sealed polyethylene bags and stored at the desired temperature. Samples were removed from storage at intervals and analyzed for phospholipid phosphorus by the procedures described previously (Tomlinson *et al.*, 1960), the homogenization of samples in 10% (w/v) trichloroacetic acid rather than in ice water being the only modification introduced.

The results are shown in Table I. Phosphorus was lost from the phospholipid fraction of the muscle at each storage temperature down to and including –30°C. Since a loss of phospholipid phosphorus has also been observed in sterile lingcod muscle stored at 20°C (Tomlinson, unpublished data), and since it now seems likely that the previously observed small losses of phospholipid phosphorus from

TABLE I. Changes in the phospholipid content of lingcod muscle during frozen storage.

Days stored	Phospholipid phosphorus (mg/g muscle) in muscle stored at:					
	–10°C		–20°C		–30°C	
	Mean[1]	Range	Mean	Range	Mean	Range
0	.22	.22–.23	.22	.22–.23	.22	.22–.23
2	.20	.19–.22	.22	.19–.26	.23	.22–.26
30	.14	.11–.16	.16	.13–.18	.23	.21–.27
90	.10	.08–.11	.12	.10–.16	.20	.19–.21
184	.08	.06–.09	.09	.07–.11	.17	.14–.21

[1]Of samples from three fish.

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iced lingcod (Tomlinson *et al.*, 1960) while not statistically significant (P = 0.05), were nevertheless real, it appears that loss of phosphorus from this fraction of lingcod muscle proceeds *post mortem* in a manner similar to that reported by Olley and Lovern (1960) for Atlantic cod.

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